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Pheromones of the Sesiidae

(formerly Aegeriidae)

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PHEROMONES OF THE SESIIDAE (formerly Aegeriidae)

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FOREWORD

The Sesiidae is a well defined family of moths which is world wide in distribution and is composed of approximately 170 genera containing over 1000 described species. Host plants which make this family economically important include ash, peach, lilac, grape, squash, rhododendron, maple, oak, strawberry, raspberry, and viburnum. The adults are diurnal and strongly mimic various Hymenoptera in both appearance and behavior. The larvae are obligate borers with endophagous habits and develop in limbs, trunks, bark, roots, and galls of trees, shrubs, and vines. Adult life is short, lasting about one week and only some have a well developed proboscis to take nectar.

North of Mexico, there are 19 genera which contain 113 species. The most recently described is Podosesia aureocinta from ash described by F. Purrington and D. Nielsen in 1977. Most of our North American species are univoltine; however, some species such as the oak borer Paranthrene simulans require more than one year for development. Most North American Sesiids have a rather narrow host preference. The dogwood borer, however, is an exception and has a very wide host range.

The initial isolation from the lesser peach tree borer and peach tree borer of two major isomeric pheromone system components, Z,Z- and E,Z-3,13-octadecadien-1-ol acetate, was reported by J. Tumlinson and coworkers in 1974 and supported in 1974 with field bioassays by C. Yonce. Cross attraction of different species was soon demonstrated by D. Nielsen which was followed by one of the most intense pheromone trapping programs of modern times. As a result of this intensive research, new species have been described and the status of others clarified.

These reports by leading researchers provide clear insight into the diversified approaches necessary to clarify the understanding of an insect's chemical communication system. They include chemistry, EAG and field responses, disruption, distribution and seasonal occurrence, trapping and trap design, and reproductive isolation.

It is fortunate that much information on Sesiid pheromones is available at this time as new technological resources become available for continued advances.

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THE CHEMISTRY OF SESIIDAE PHEROMONES

J. H. Tumlinson^{1/}

INTRODUCTION

The initiation of an investigation into the chemistry of the lesser peachtree borer, Synanthedon pictipes (Grote and Robinson) (LPTB), and peachtree borer, Synanthedon exitiosa (Say) (PTB), pheromones was prompted by several factors in addition to the economic importance of these pests. We chose these moths to serve as models for the study of pheromones and behavior and for the design of insect pest control systems based on the utilization of pheromones and behavior modification. It appears that our choice was well founded since several scientists in the United States, Europe, and Japan have subsequently studied the responses of many Sesiidae species to the pheromones we identified and at least one project to design a pest management system for LPTB and PTB based on the use of pheromones is now underway.

Although the identification and synthesis of these pheromones is a recent development, females of the LPTB have been known for more than 70 years to produce a pheromone that attracts conspecific males (Girault 1907). Cleveland and coworkers (Cleveland and Murdock 1964, Cleveland et al. 1968, Wong et al. 1972) demonstrated the potential of this pheromone in monitoring and trapping males by using females in traps. Our subsequent studies of these insects' behavioral responses to their pheromones have been facilitated because they are diurnal and are relatively easy to observe in their natural habitat. Thus native wild insects that are on the wing from March to October in the Southeastern United States can be used in bioassays and behavioral studies. This eliminates many of the problems associated with the use of lab reared insects for such studies.

ISOLATION AND IDENTIFICATION

The bioassays used to monitor the isolation of this pheromone were conducted in the field by placing each sample to be tested in a petri dish on the ground in a peach orchard (Yonce et al. 1974). Responses of flying, wild males to extracts and various fractions were observed and compared to the response to caged, live, virgin females. These responses typically consisted of an upwind approach, hovering, and making contact

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with the cage containing virgin females or the dish containing active substances. The advantages of this test were that it was simple, rapid, and the complete repertoire of behavioral responses of the males to the pheromone could be observed. Later, trapping studies with synthetic pheromones indicated that there are subtleties in the behavior of these species that may be overlooked even in bioassays of this type (Nielsen et al. 1975, Barry et al. 1978).

The isolation and identification of the pheromones of the LPTB and PTB were described by Tumlinson et al. (1974). The pheromones were obtained by extracting the ovipositors of 1- and 2-day-old virgin female LPTB and PTB with methylene chloride and pentane, respectively. The ovipositors of 25,000 lab reared LPTB females and 800 PTB females that emerged from field-collected pupae were processed this way. The extracts were concentrated by distillation, and the active components were purified by liquid (LC) and gas chromatography (GC). The purity of the active component obtained from each species was verified as greater than 99.5% by analysis on several GC columns including a 60 m Dexsil capillary column and a 45 m DEGS support-coated, open tubular column. However, at that time available analytical methods would not completely resolve all the isomers of 3,13-octadecadien-1-ol acetate (ODDA). Thus it is possible that the isolated pheromones could have contained as much as 4% of an undetected isomeric impurity.

The active compounds were identified by mass and infrared spectra and by microozonolysis and hydrogenation. The PTB pheromone was shown conclusively to be ZZ-ODDA, and the LPTB pheromone to be one of the other isomers. After synthesis of all four isomers (see later), EZ-ODDA was determined to be identical to the LPTB pheromone. Additionally we found that as little as 1% of the ZZ-isomer, present as an impurity in the EZ-ODDA, significantly reduced the response of LPTB males to their synthesized pheromone. Subsequently, Nielsen and coworkers (Nielsen et al. 1975, Barry et al. 1978) discovered that more PTB males are captured in traps baited with ZZ-ODDA containing ca. 4% EZ-ODDA than in traps baited with pure ZZ-ODDA.

It is worth noting that during the initial LC purification of the LPTB extract, a fraction that eluted after the active pheromone, and in the region that alcohols would be expected to elute, attracted males of another species, Synanthedon rileyana (Hy. Edwards). This fraction was not attractive to LPTB males and did not appear to influence their response to the active fraction. However, this suggests that the LPTB female produces an alcohol, possibly closely related structurally to the pheromone, whose function in the chemical communication system of these insects is not understood. This component was not isolated and identified.

SYNTHESIS

Four ODDA isomers were synthesized in our laboratory by R. E. Doolittle (Doolittle et al. 1979, Tumlinson et al. 1974) following the routes outlined in figure 1. The major difficulty in synthesizing these

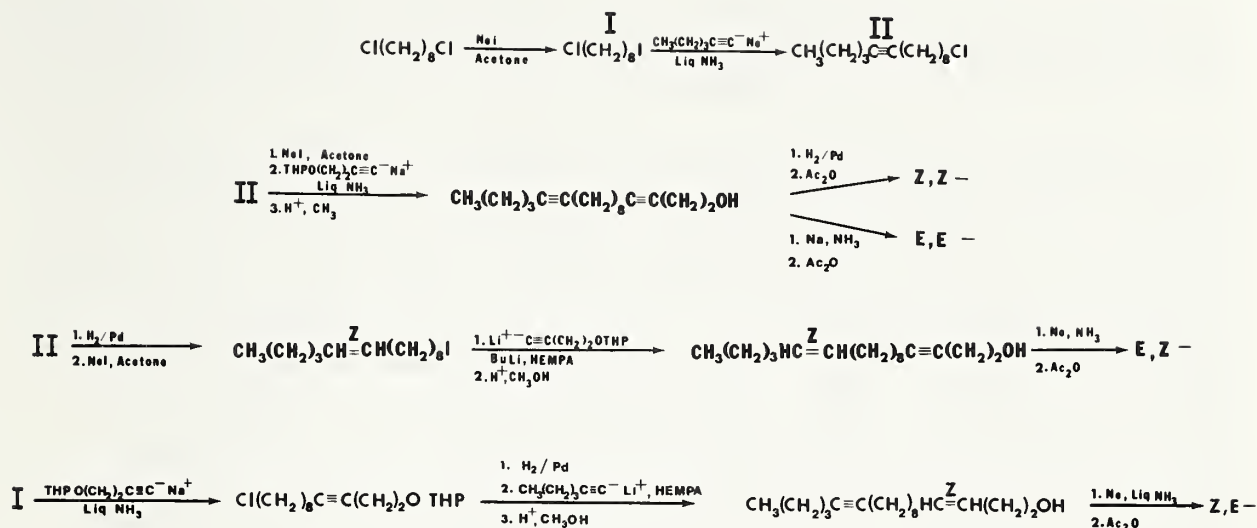


Figure 1.--Scheme for synthesizing the four isomers of 3,13-octadecadien-1-ol acetate (ODDA).

compounds has been to produce the desired geometrical isomer in very high purity. In particular it is extremely difficult to produce the trans (E) configuration about the olefinic bond at the 3-position without also producing about 2-3% of the cis (Z) isomer at this position. Thus the EZ-ODDA always contains at least 2-3% ZZ-ODDA which must be removed by AgNO₃ liquid chromatography to obtain a product attractive to LPTB males. For large quantities of pheromone this is a very time consuming and expensive process.

Underhill et al. (1978) prepared ZZ-ODDA and Uchide et al. (1978) described the synthesis of ZZ- and EZ-ODDA. Voerman (1979) has also developed syntheses for EZ-, ZZ-, and EE-ODDA. The yields in Voerman's syntheses are very good but the problem of purification of the EZ-ODDA to remove the ZZ-isomer still remains.

Work now in progress (R. E. Doolittle, personal communication) with newly developed catalysts and synthesis techniques shows considerable promise for producing the ODDA isomers in greater than 99% purity. When this work is complete the isomerically pure compounds should be available in large enough quantities for field experiments.

IMPROVED ANALYTICAL METHODS

The inactivity of what we originally perceived as pure synthetic EZ-ODDA for trapping LPTB males forced us to take a very critical view of our analytical methods and purification techniques. This was the initial stimulus that led us into the area of high-efficiency, high-

resolution liquid chromatography, and later into high-efficiency capillary gas chromatography. The isomers of ODDA are still the most difficult to separate of any of the geometrical isomers with which we have dealt.

Previously AgNO_3 -coated silica had been used in gravity-flow liquid chromatography columns and on thin-layer plates to separate olefinic isomers. Our initial high pressure columns were dry-packed with a 20% AgNO_3 -coated silica (2-11 μm particle size) and eluted with benzene (Heath et al. 1975, Tumlinson and Heath 1976). These columns effectively separated the EZ- and the ZE- from the ZZ-ODDA although they did not separate EZ- from ZE-ODDA (fig. 2). With 1 in. (o.d.) columns of this type we were able to inject 200 μg samples and remove all ZZ- from EZ-ODDA and vice-versa. Since the synthesis procedure for EZ-ODDA produces only a fraction of a percent of ZE-ODDA, this method was satisfactory for purification of all the isomers. In this way we obtained several grams of each isomer in greater than 99.5% isomeric purity. Subsequently we developed a slurry packing technique using microparticulated silica that produced LC columns with greatly improved resolution (Heath et al. 1977). Additional benefits were greater sensitivities and shorter analysis times. Heath discovered that the relative partition ratios of the various isomers could be varied by varying the percent loading of AgNO_3 on the silica. Thus we were able to effect complete resolution of all four ODDA isomers on a 10 cm, 5% AgNO_3 loaded column (fig.3). This gave us the analytical capability we needed to precisely define the isomeric content of the synthesized ODDA isomer.

Our most recent efforts in analytical chemistry have been directed toward the development of high efficiency GC columns to separate pheromone isomers. A glass capillary column has been developed that will separate all four isomers of ODDA (fig. 4) (Heath et al. 1979). This technique enables us to accurately analyze commercial batches of the various ODDA isomers to determine the percent of isomeric impurities. Additionally, further development of this technique with splitless capillary GC (Grob and Grob 1978) should facilitate the analysis of pheromones from small numbers of females of other Sesiidae species.

FORMULATION

Dr. J. H. Cross of our laboratory has calculated that the vapor pressure of ODDA is about 1×10^{-9} mm at 24 °C and the boiling point at atmospheric pressure is about 490 °C (J. H. Cross, personal communication). Thus it is obvious that these compounds have very low volatilities.

In initial tests, traps baited with rubber bands or rubber septa impregnated with synthetic pheromone caught more male LPTB than those baited with pheromone on other substrates including polyethylene vial caps, cotton wicks, sand, and tygon tubing (Yonce et al. 1976). Subsequently most investigators have baited traps with rubber septa or rubber bands loaded with 10 to 1000 μg of pheromone. Most studies have indicated that increasing the amount of pheromone on a septum increases

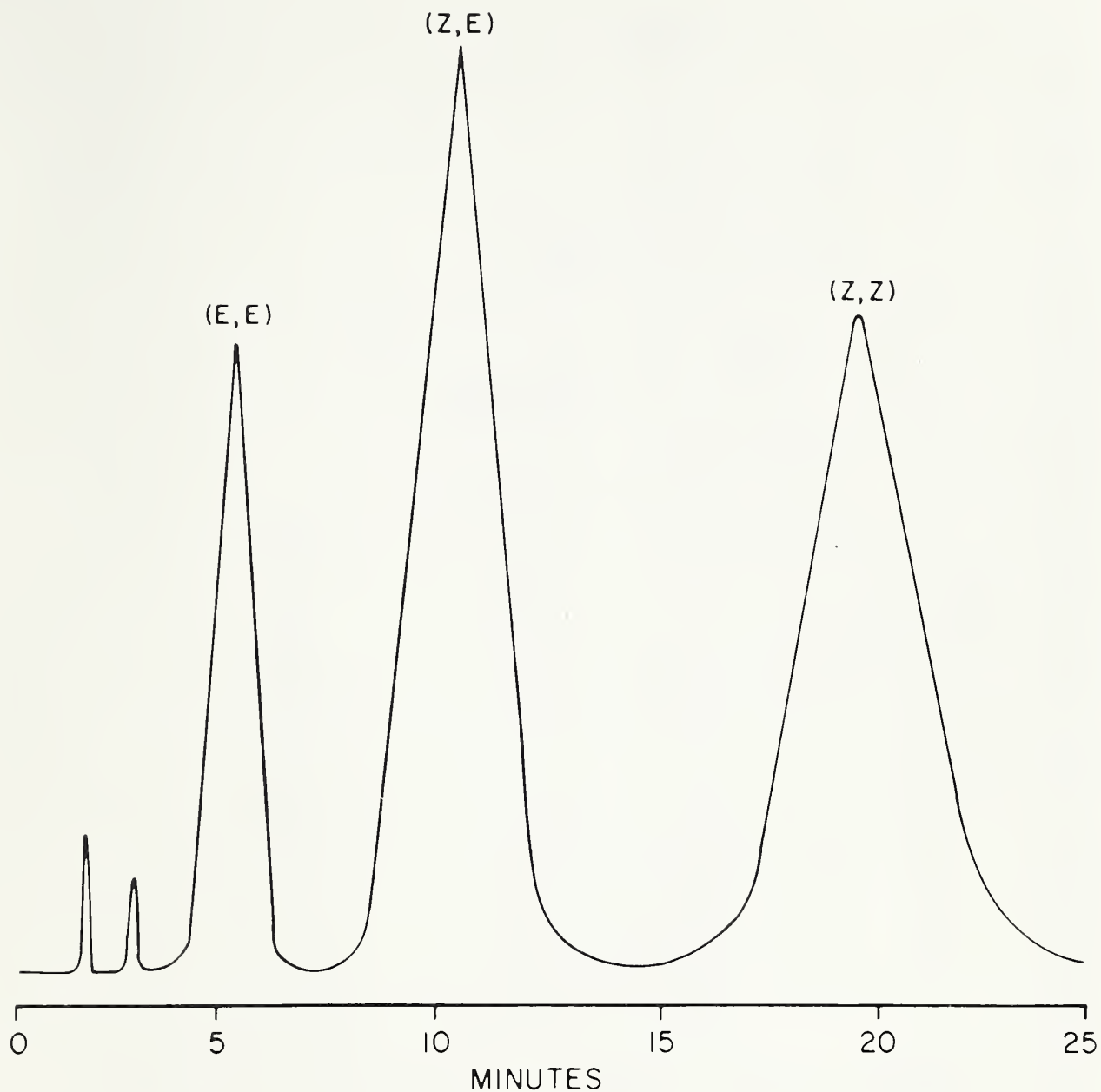


Figure 2.--LC separation of (E,E), (Z,E), and (Z,Z)-3,13-octadecadien-1-ol acetate. Column 50 cm x 9.3 mm i.d.; 20% AgNO₃-silica, particulate size, 2-11 μ m; mobile phase benzene; pressure, 4500 psi; flow 6.0 ml/min; detector refractive index; sample size, 100 mg.

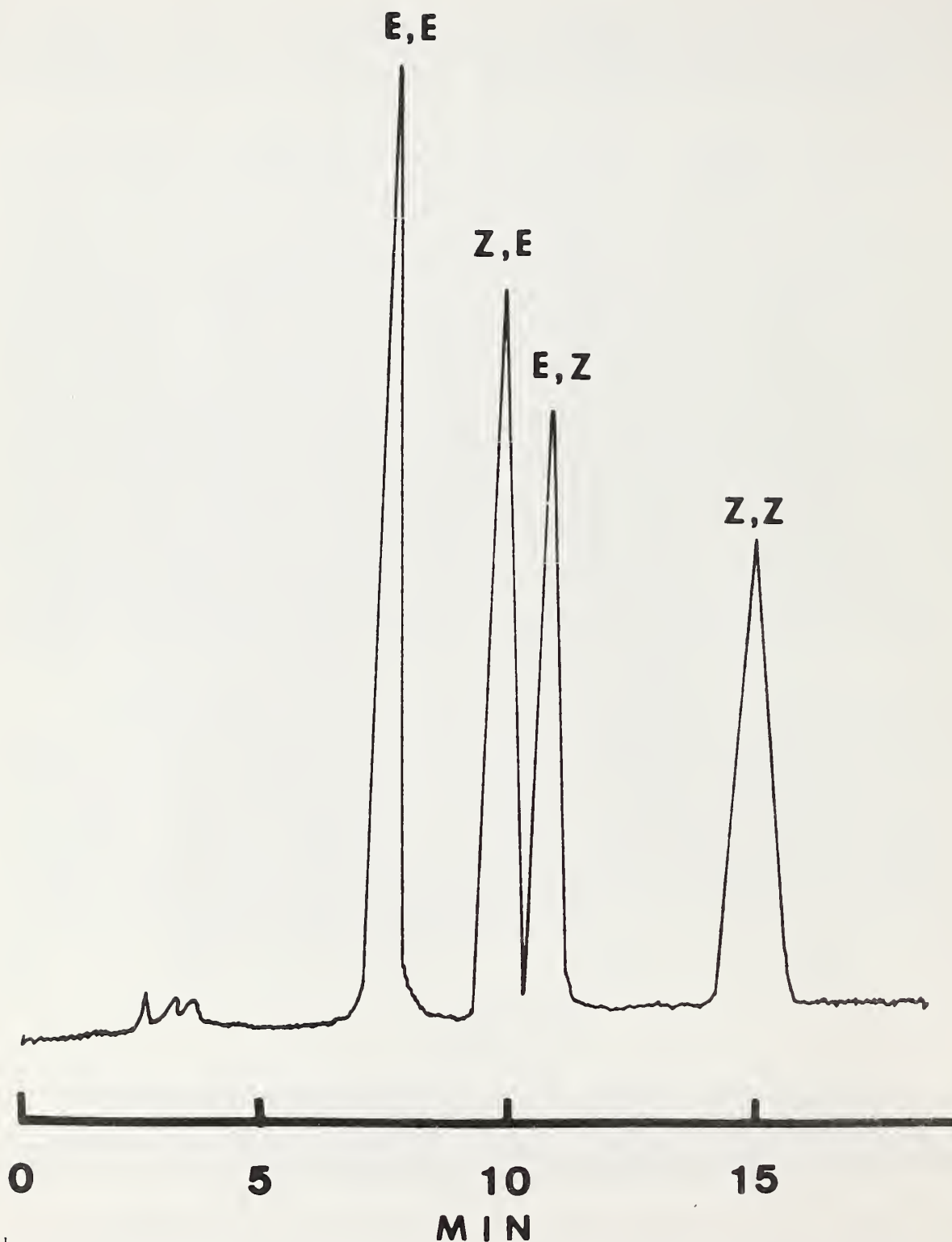


Figure 3.--LC separation of the four isomers of 3,13-octadecadien-1-ol acetate. Column 10 cm x 4.4 mm i.d.; 5% AgNO₃-silica, particle size, 5 um; mobile phase benzene; flow, 0.8 ml/min; detector refractive index; sample size 50 ug each isomer.

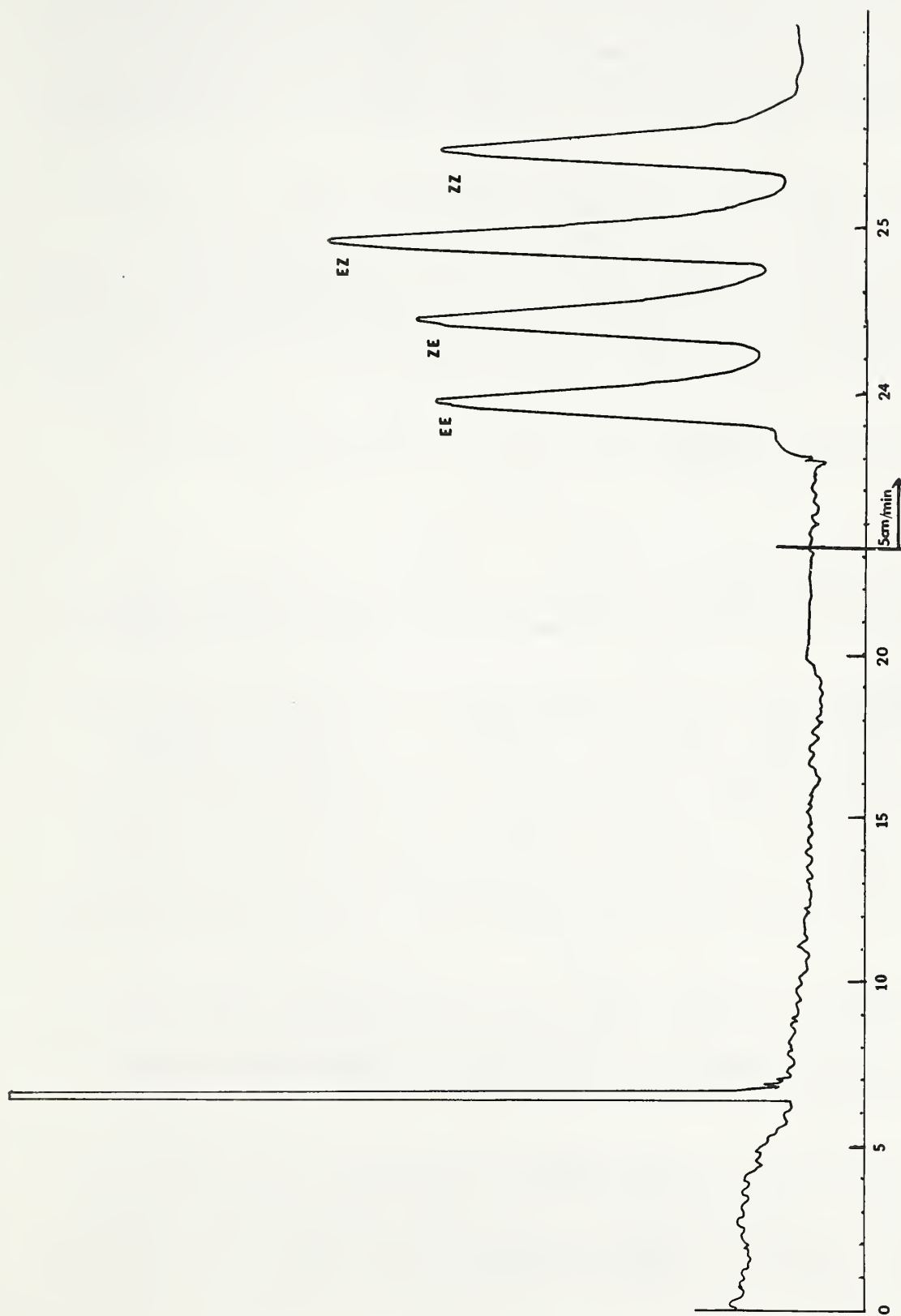


Figure 4.--Capillary GC separation of the four isomers of 3,13-octadecadien-1-ol acetate. Column 60 m x ca. 0.25 mm i.d.; glass; stationary phase SP 2340; column temperature 190 °C; He carrier gas flow 18 cm/sec; split ratio 50:1; sample size ca. 0.4 ug each isomer.

trap capture until the trap capacity is exceeded. Yonce baited a large trap with 10 septa, each loaded with 1 mg of pheromone, and captured an average of 22,805 male LPTB per year for 3 years without renewing the bait (C. E. Yonce, personal communication). Each fall the septa were removed from the trap and stored in a refrigerator until they were placed back in the same trap in the spring. Sticky inserts were replaced in the trap as they became covered with male moths.

These pheromones have also been formulated in Conrel hollow fibers and Hercon plastic strips and the results have been similar to those with rubber septa in trapping studies. Release rate measurements by J. H. Cross (unpublished data) indicate that both types of commercial formulations are releasing only about 0.05 μg of pheromone per hour at 25 °C although they were designed to release 5 $\mu\text{g}/\text{h}$. Additionally these studies have shown that release rates measured in the laboratory can be used to predict relative trap captures in the field.

Presently an ideal formulation for these low volatility compounds is not available. Available data indicates a successful formulation should have a large surface area to facilitate volatilization.

FUTURE DIRECTIONS

There are at least four areas in which further chemical research should prove fruitful. Most of these have been alluded to in my previous remarks.

There is still much to be done to elucidate and clearly define the chemical communication systems of the LPTB and the PTB. The geometrical and functional isomers that make up the complete pheromones of these species should be isolated and identified. Additionally, compounds that may act as inhibitors for other species or play some other role in species isolation and interaction should be investigated. The analytical methods necessary to support most of this research are now available. Obviously this chemical research will require the support of biologists interested in detailed behavioral analyses and probably electrophysiological studies.

The components of the pheromones of other Sesiidae species, particularly the more common ornamental pests, should be isolated and identified. A careful chemical definition of the pheromones of these species rather than an empirical approach to discovering attractants should produce better results.

A formulation that will release ODDA at rates of 5 $\mu\text{g}/\text{h}$ or greater at 25 to 35 °C for 4 to 6 months would be very useful. This formulation would be useful for other pheromones of high molecular weight including the large hydrocarbons produced by many Diptera species and the pheromones of the fall webworm moth, Hyphantria cunea (Drury), (Hill et al. 1979), and the saltmarsh caterpillar moth, Estigmene acrea (Drury), (Hill and Roelofs 1979).

Finally, although Doolittle's improved synthesis shows promise of producing EZ-ODDA pure enough for field trapping LPTB males, it requires some purification steps. Better, more commercially adaptable syntheses, that would make the ODDA isomers available in pure form to field biologists, are still needed. The high degree of purity required for activity in some cases make this a particularly difficult and challenging subject for investigation.

ACKNOWLEDGEMENT

The author thanks Dr. R. E. Doolittle and Mr. R. R. Heath for their cooperation in developing the syntheses and analytical methods, respectively, for all the ODDA isomers. The cooperation of all the entomologists who have studied Sesiidae behavior in response to pheromones during the past 6 years including but not limited to most of the participants in this symposium is also greatly appreciated.

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EAG AND FIELD RESPONSES OF SESIID MALES TO
SEX PHEROMONES AND RELATED COMPOUNDS^{1/}

D. G. Nielsen, F. F. Purrington, and G. F. Shambaugh^{2/}

Several early workers reported observations on sexual behavior of sesiids. Hulst (1882) reported that male lilac borers, Podosesia syringae (Harris), (1882) and raspberry crown borers, Pennisetia marginata (Harris), (1883) are attracted to their respective females. Lesser peachtree borer, Synanthedon pictipes (Grote & Robinson), males were observed to be attracted to conspecific females in the characteristic display position (Girault 1907). King (1917) reported that fluid from lesser peachtree borer female genitalia was attractive to conspecific males. Gossard and King (1918) published a photograph of a peachtree borer, Synanthedon exitiosa Say, female exposing her scent glands to attract males. Engelhardt (1946) and J. H. Newton, state entomologist in Colorado, working separately, used virgin female cottonwood crown borers, Sesia tibialis (harris), to attract males. Sex attraction was observed with the hornet moth, Sesia apiformis (Clerck), in the area surrounding New York City, and Melittia snowii Hy. Edwards near San Antonio, Texas (Engelhardt 1946). Engelhardt also reported that grape root borer, Vitacea polistiformis (Harris), and Paranthrene asilipennis (Boisduval) males were strongly attracted to their respective females.

These observations were recorded at a time when biologists were actively cataloging our biota and recording observed biological events. During that time chemists did not have the capability to determine molecular structures of attractant odors. Consequently, knowledge of sex attraction was used only to facilitate collection of males by exposing females in screen field cages. Only response to conspecific males was reported, and there was apparently no thought given to the potential for developing control measures based on sexual behavior. Much later, early key pheromone chemistry was conducted with a beneficial insect, not a pest species (Butenandt et al. 1959).

Our initial interest in sexual response of male clearwing moths resulted from efforts to develop improved control measures for insects that construct galleries in trees and shrubs (Nielsen 1973). Cleveland and Murdock (1964) initiated studies with natural sex attractant of lesser peachtree borer to (1) determine if large numbers of males could be captured in sticky traps baited with virgin females and (2) locate the source of pheromone within the female. Wong et al. (1972) attempted to mass trap lesser peachtree borer males with sticky traps baited with virgin females. We discovered that caged virgin female lilac borers attracted both conspecific males and male

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Paranthrene simulans (Grote) (Nielsen and Balderston 1973). Subsequently, we began evaluating attractiveness of fractions of lesser peachtree borer female abdominal tip extracts when Tumlinson and co-workers initiated pheromone chemistry research with this species (Tumlinson et al. 1974). Eventually, we evaluated attractiveness of pure isomers of 3,13-octadecadien-1-ol acetate (ODDA) and corresponding alcohols (ODDOH), separately and in combination (Nielsen et al. 1975, 1978; Nielsen and Purrington 1978a,b). Later, we developed electroantennogram (EAG) capability to expedite development of attractants for economically important clearwings (Nielsen and Purrington 1978b). This paper reports a summary of our work and includes published reports of others.

METHODS AND MATERIALS

Fractions of lesser peachtree borer female abdominal tip extracts were collected at specified intervals from a liquid chromatography column, diluted to specified female equivalents in pentane, and placed in small ampoules by Tumlinson and co-workers. Ampoule contents were exposed for evaluation by breaking the top from an ampoule and pouring its contents into a watch glass. Fractions were evaluated at selected locations throughout northeastern Ohio at times coinciding with emergence of certain clearwing species. Sometimes, fractions were exposed in presence of caged, calling clearwing females. At other times, females were simply used to confirm presence of males and then placed in a cooler before fractions were evaluated (Nielsen et al. 1975). Responding males were captured, identified, and recorded.

Purified, synthetic E,Z-ODDA and the other three geometrical isomers were evaluated for attractancy to lesser peachtree and peachtree borer, lilac borer, and Paranthrene simulans by exposing isomers singly in watch glasses or placing a small amount of one compound on a rubber band or rubber septum. When a series of candidates was evaluated at the same time, each was placed in a separate container, and containers were spaced ca. 5-10 m apart in a line perpendicular to prevailing winds. If the material to be evaluated was placed in a sticky trap, only captured clearwings could be counted as responders. If the "bait" was simply positioned on the ground, on a table, or on top of a stake, an observer recorded the male response in terms of (1) flight to the general area, (2) hovering near the attractant source, or (3) mating attempts (= striking). During the course of these evaluations, representatives of all species of responding males were captured and identified. T. D. Eichlin, Calif. Dept. of Food and Agric., Sacramento, identified representatives of all species captured.

Pherocon 1C traps were baited with pure isomers or with commercial preparations containing ca. 90% Z,Z-ODDA and various amounts of the other three geometrical isomers. We also mixed pure Z,Z- and E,Z-ODDA in combinations to determine optimum blending for various species (Barry et al. 1978). Eventually, all four ODDA isomers and corresponding alcohols were supplied by Tumlinson for evaluation. All isomers were evaluated in the aforementioned manner, sometimes with cooperators in several parts of the U.S. (Nielsen and Purrington 1978a, 1978b, Nielsen et al. 1978).

Electroantennograms were accomplished in a radio frequency-shielded, grounded room. An antenna was removed from the moth with a pair of forceps. An attempt was made to obtain muscle tissue attached to the base of the antenna. The antenna was stuck at an acute angle to the inside of a ring of tacky wax in a petri dish. The tacky wax ring formed a cup with a Grass type E-1B silver disc electrode as the bottom. The bottom of the antenna was immersed in Caltec saline (Caltec and Sattelle 1973) in the cup. The distal tip of the antenna was clipped with iridectomy scissors, and a recording glass microelectrode (Ag-AgCl wire in saline) was lowered over the cut tip of the antenna with a micromanipulator.

Both electrodes were connected to a Grass Polygraph using a 7 PL-A D.C. preamplifier and a D. C. driver amplifier. A permanent record was made of the electroantennogram. The magnitude of the initial drop in voltage after stimulation was measured.

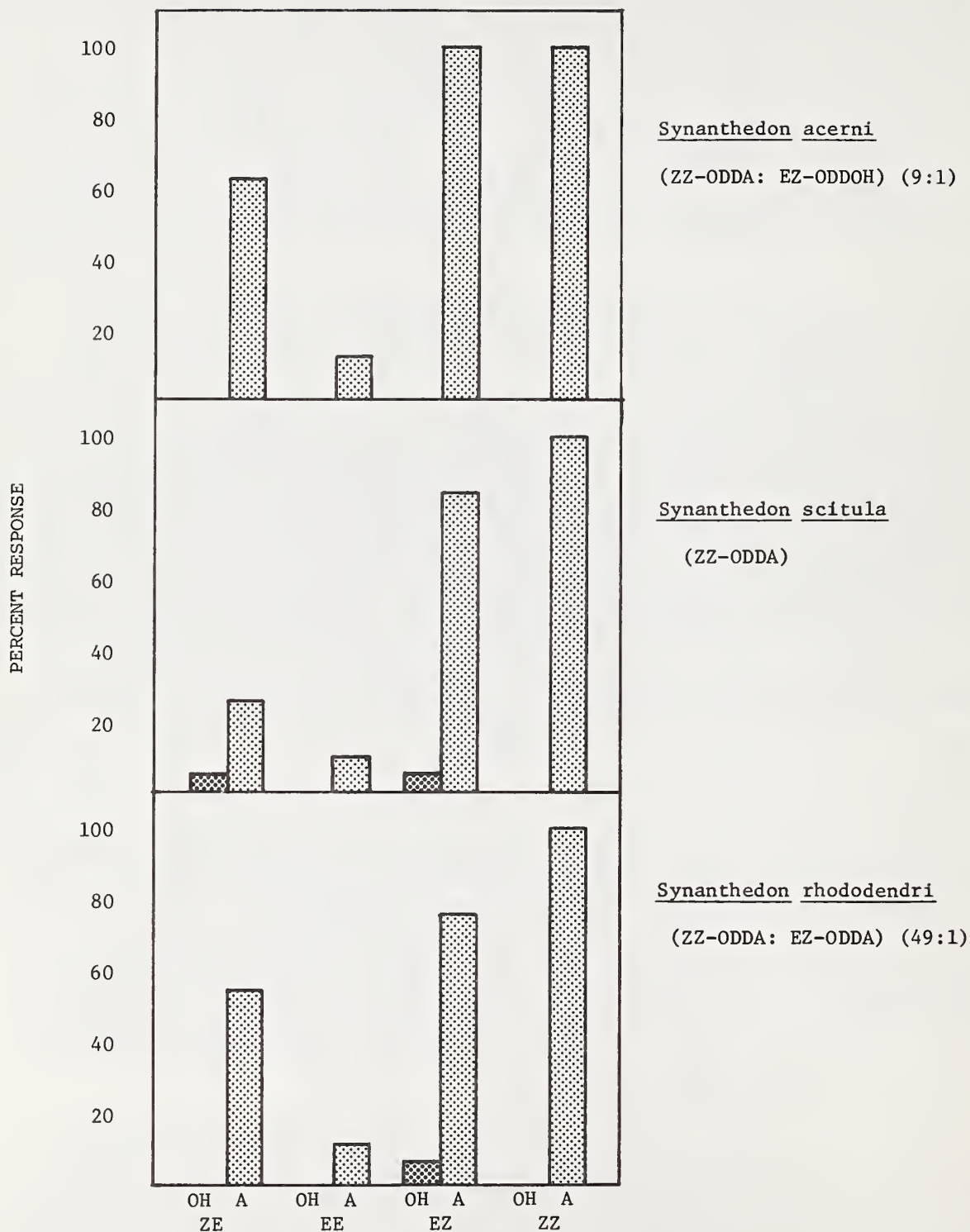
Laboratory air was purified through charcoal and humidified in a gas washing bottle before blowing over the antenna from a glass delivery tube (5 mm diam.). Candidate chemical compounds were diluted to 1 µg/ul, added to small pieces (1 cm²) of filter paper and placed into glass Pasteur capillary pipets. When ready to be used, the pipet was fitted inside a sleeve-type rubber stopper attached to the needle end of an 8 cc glass syringe. The tip of the pipet was inserted into the side of the delivery tube. A 4 cc air puff containing the candidate chemical was injected to the 200 cc/min. flowing air stream. A flexible hose (6 cm diam.) was positioned behind the preparation so that chemicals in the flowing air would be removed from the recording room by vacuum. Three or more replicates were obtained for each treatment/antenna.

RESULTS

EAG Response

All eight isomers of 3,13-ODDA and 3,13-ODDOH were screened for clearwing male EAG activity (figs.1-4). Five isomers elicited responses significantly greater than blanks, but only Z,Z- and E,Z-acetates and alcohols have proven to be important constituents of sex attractants developed to date. Although Z,E-ODDA elicited significant EAG response in Synanthedon acerni, S. rhododendri, and S. pictipes, extensive field tests at several locations have failed to demonstrate importance of this isomer in increasing lesser peachtree borer trap capture (McLaughlin et al. 1977, Nielsen and Purrington unpublished). Its potential importance as a sex pheromone component for other clearwings has not been demonstrated.

Although our EAG data neither reveal which isomers are attractants or repellents nor indicate relative proportions of isomers necessary to achieve a useful bait, they do indicate which compounds stimulate the antenna. This information identifies compounds that do not appear to be promising candidates for field work. Furthermore, we have found good correlation between the major attractant component and greatest EAG response. The compound eliciting the second highest response may be either an important constituent at a low level, as in Synanthedon exitiosa (fig. 5), or a repellent, as in S. pictipes (fig. 4).



Isomers of 3,13-ODDOH(OH) and ODDA(A)

Figure 1.--EAG responses of male clearwing moths, Synanthedon acerni, S. scitula, and S. rhododendri. Responses were standardized by calculating their magnitude as a percentage of the response to (Z,Z)-ODDA (=100%).

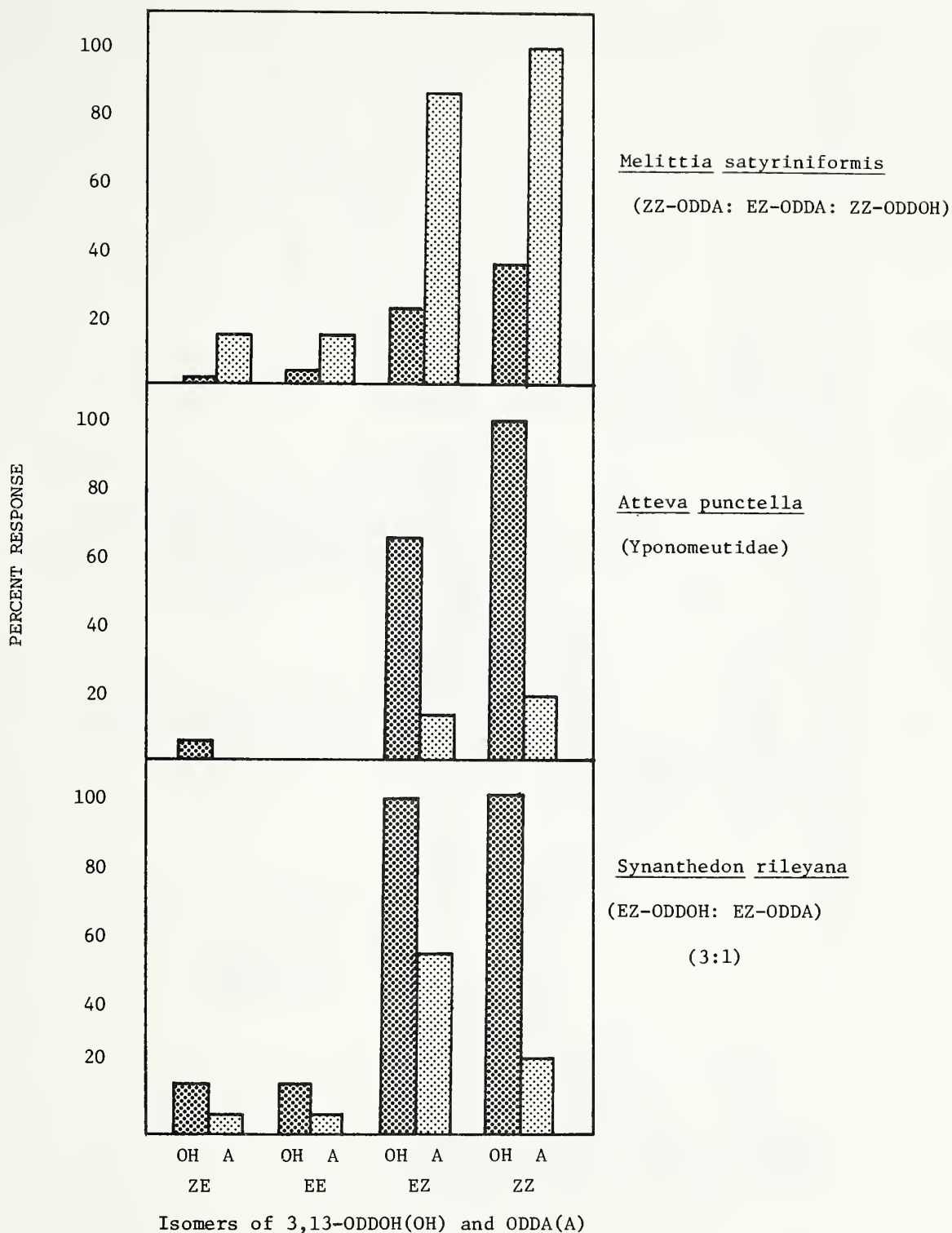
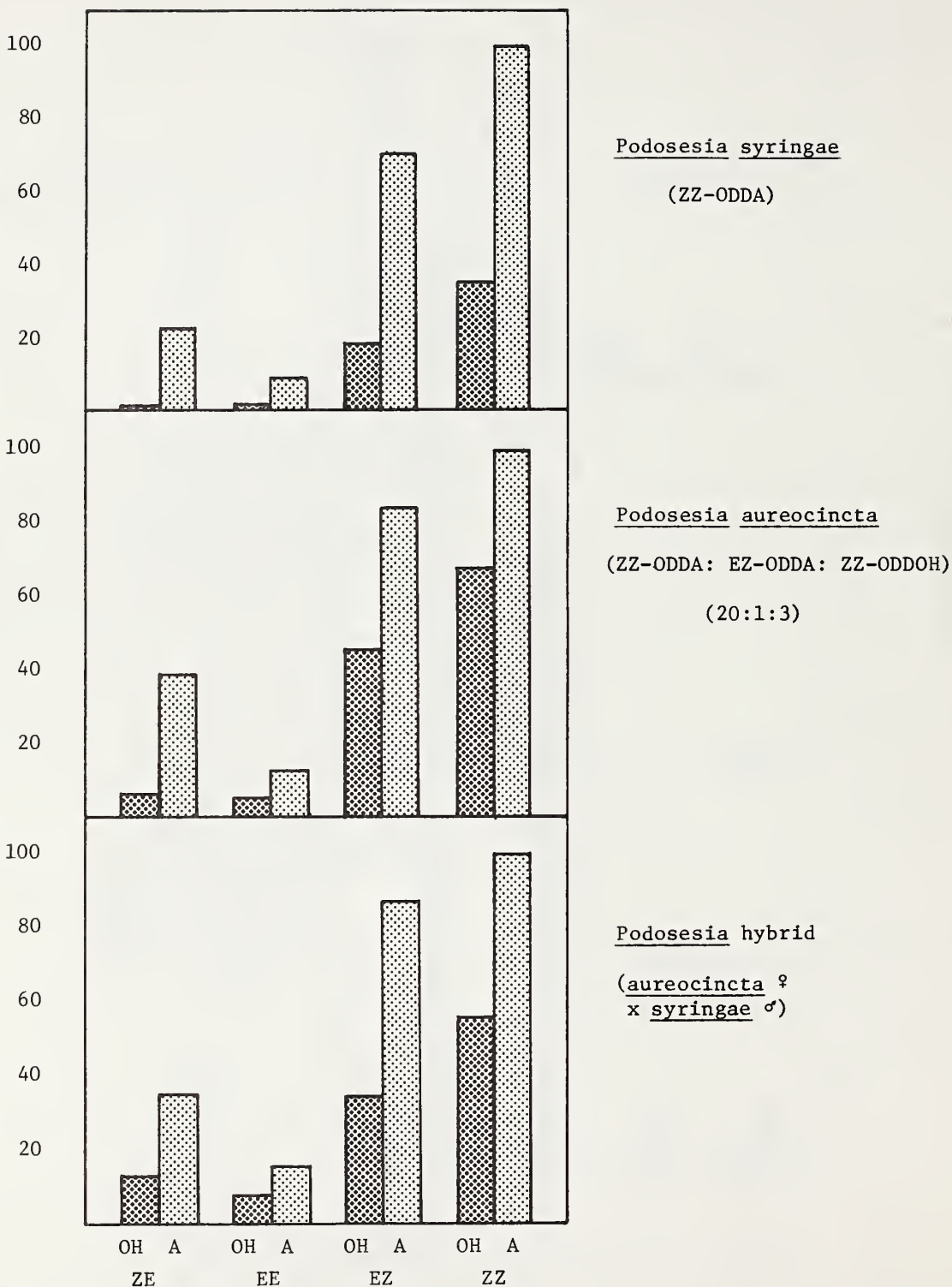


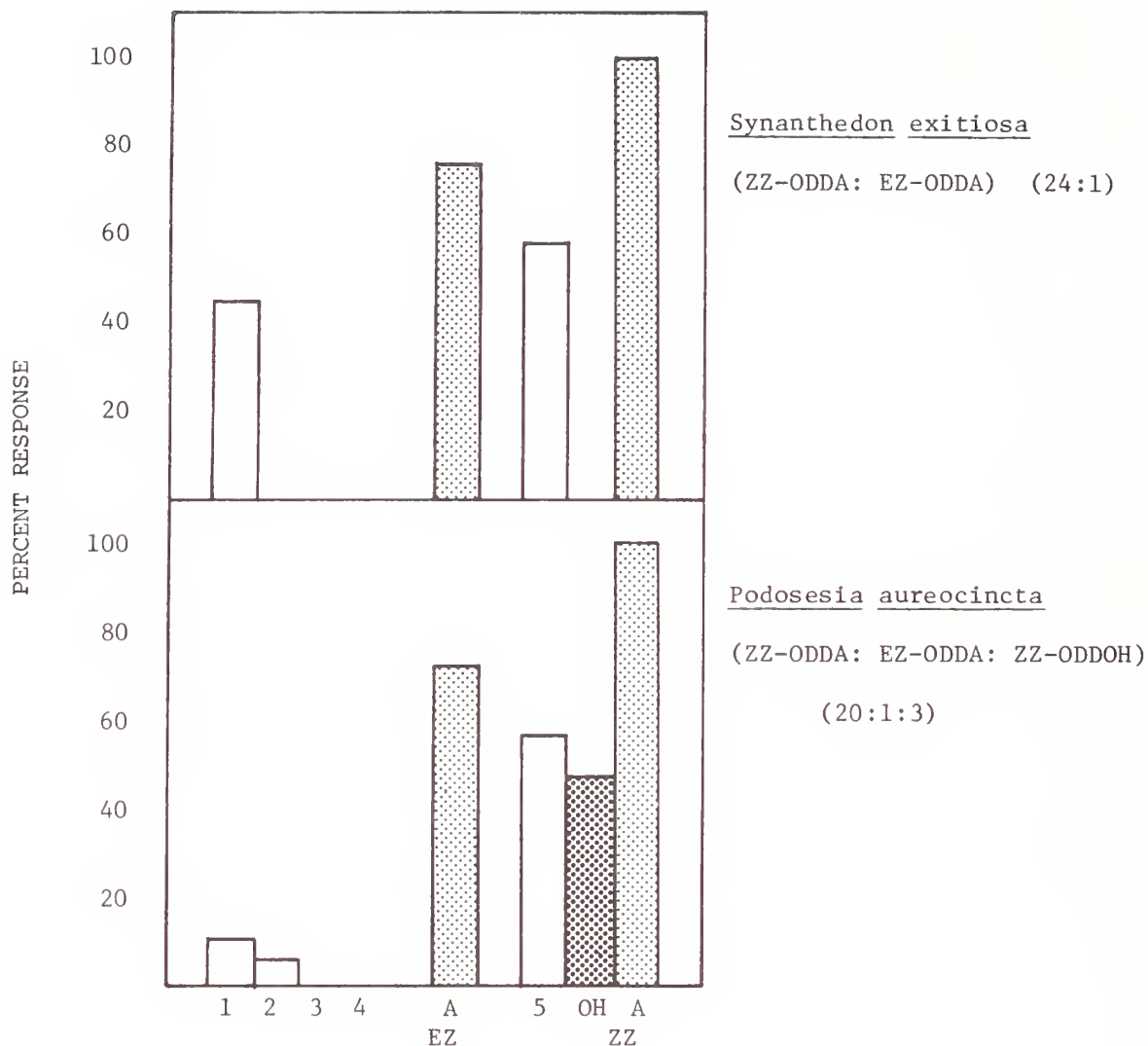
Figure 2.--EAG responses of two clearwing male moths, Melittia satyriniformis and Synanthedon rileyana, and of Atteva punctella, a member of the same superfamily. Responses were standardized by calculating their magnitude as a percentage of the response elicited by the most active isomer (=100%).

PERCENT RESPONSE



Isomers of 3,13-ODDOH(OH) and ODDA(A)

Figure 3.--EAG responses of two *Podosesia* spp. males and hybrids between the species. Responses were standardized by calculating their magnitude as a percentage of the response to (Z,Z)-ODDA (=100%).



1. 3,6-Dioxadecanyl ethanoate
 2. olealdehyde (Z-4-octadecenal)
 3. methyl linoleate
 4. ethyl linoleate
 5. (Z,Z)-3,13-octadecadienal
- EZ-A (E,Z)-ODDA
 ZZ-A (Z,Z)-ODDA
 ZZ-OH (ZZ)-ODDOH

Figure 5.--EAG responses of male Alcathoe caudata, Synanthedon pictipes, S. acerni, S. exitiosa, and Podosesia aureocincta, to (Z,Z)-ODDOH and -ODDA, (E,Z)-ODDA, and other straight chain hydrocarbons (1-5). Responses were standardized by calculating their magnitude as a percentage of the response elicited by the most active compound (=100%).

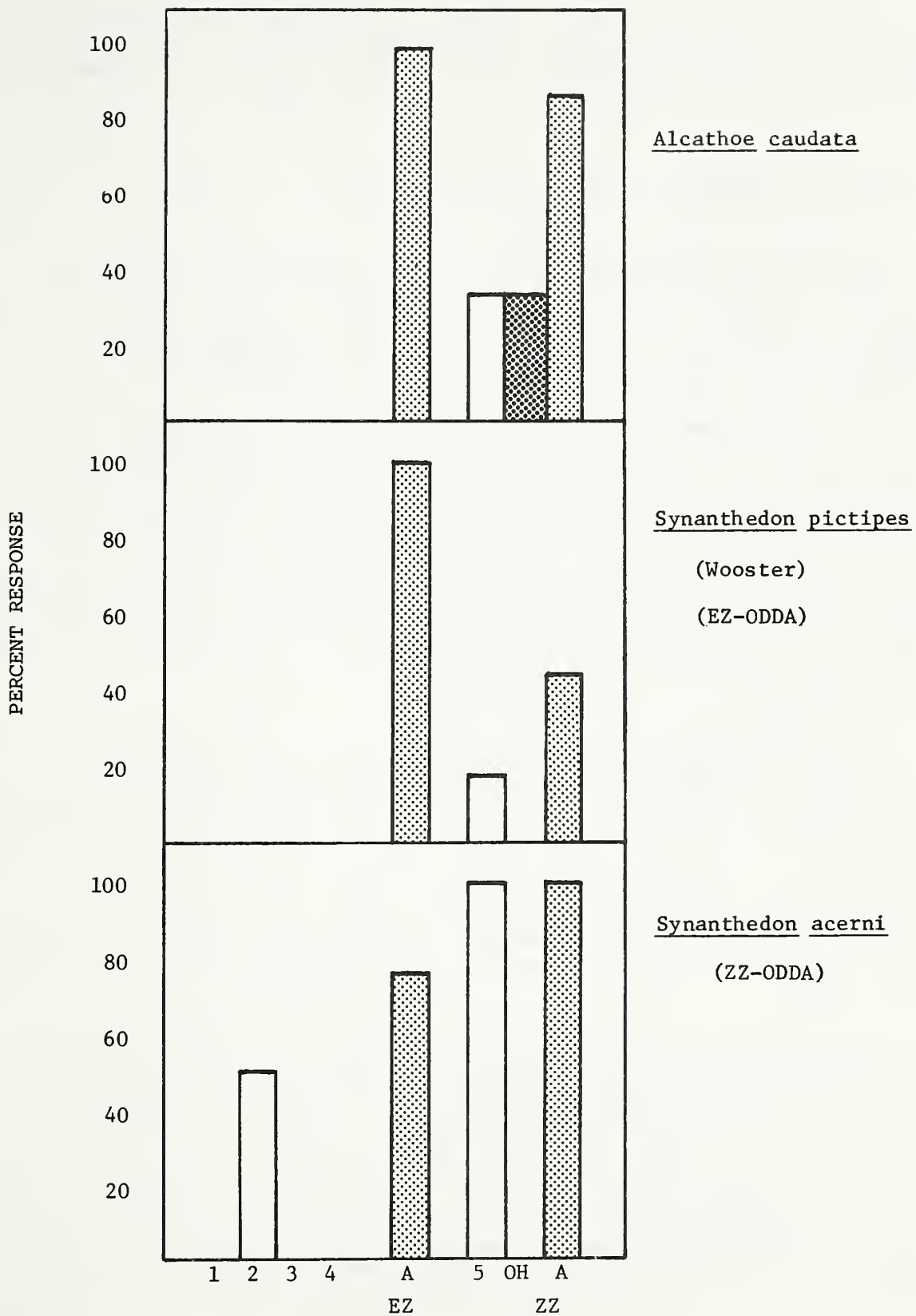


Figure 5 (continued).

Alcohols elicited stronger responses than acetates in Synanthedon rileyana and Atteva punctella (ailanthus webworm: Lepidoptera:Yponomeutidae), a moth closely related to clearwings. We have evaluated trap baits for attractiveness to S. rileyana but not to A. punctella (fig. 2).

Although acetates elicited significantly greater responses than alcohols in M. satyriniformis, Z,Z-alcohol may be an important component in its sex attractant (fig. 2).

EAGs of both Podosesia spp. were qualitatively similar, but Z,Z- and E,Z-alcohols elicited significantly greater response in P. aureocincta (fig. 3) (Nielsen and Purrington 1978b). The Z,Z-alcohol, along with E,Z-acetate proved to be important constituents in the aureocincta sex attractant, whereas Z,Z-acetate is an effective trap bait for syringae. Hybrid males (aureocincta ♀ x syringae ♂) gave intermediate responses to EAGs (fig. 3).

We measured EAG responses of males in five clearwing species to E,Z- and Z,Z-acetates and alcohols, two commercial esters, and three other materials synthesized by H. S. An, J. P. Robinson and L. W. Haynes at The College of Wooster (fig. 5). Two aldehydes, one monounsaturated and one doubly unsaturated, elicited dramatic responses in S. acerni. Z,Z-ODDAL elicited strong responses in P. aureocincta and S. exitiosa. The aldehyde did not appear to mimic the alcohol, its precursor, since it elicited strong responses from species that do not respond to alcohols (i.e., S. exitiosa and S. acerni). These results suggest that some clearwing males may have antennal receptors specific for aldehydes.

Field Response

Evaluations based on counting males flying in the vicinity of dishes containing candidate compounds confirmed that E,Z- and Z,Z-ODDA were attractive to lesser peachtree borer and peachtree borer males, respectively, as reported by Tumlinson et al. (1974). However, when these isomers were evaluated as trap baits, E,Z remained active while Z,Z failed as a trap bait for peachtree borer males (Nielsen et al. 1975). At the same time, a commercial preparation of Z,Z-ODDA, contaminated with other isomers, was an excellent trap bait for this species. Subsequently, we determined that a 96:4 ratio of Z,Z to E,Z optimized capture of peachtree borer males (Barry et al. 1978).

A fraction (fraction A) of lesser peachtree borer extract that was unattractive to lesser peachtree borer males attracted 2 different species of clearwing moths, Synanthedon rileyana (Hy. Edwards) and Podosesia aureocincta Purrington and Nielsen (Nielsen et al. 1975). Although fraction A was not characterized chemically, Tumlinson indicated it eluted from the chromatographic column at a time when alcohols were expected (personal communication). Consequently, Tumlinson and co-workers synthesized and purified all four geometrical isomers of 3,13-octadecadien-1-ol (ODDOH). Subsequent trapping studies with ODDA's and ODDOH's lend support to the contention that fraction A was a precursor alcohol in lesser peachtree borer female extract.

In our studies, a 3:1 mixture of E,Z-ODDOH and E,Z-ODDA proved to be the best trap bait for S. rileyana, a non-economic clearwing that feeds on horse-nettle, Solanum carolinense L. (unpublished). Z,Z-ODDOH is an important constituent of the three-component bait developed for P. aureocincta (Nielsen and Purrington 1978b).

Alcohols are important constituents of sex pheromones of other clearwing moth pests. Underhill et al. (1978) presented trapping data indicating that a mixture of ODDA and ODDOH is an excellent trap bait for the cottonwood crown borer, Sesia tibialis (Harris). Their EAG data with pure isomers and fractions of female abdominal tip extracts indicate "that the synthetic sex attractant developed for this species is similar to, if not identical with, the natural sex pheromone of S. tibialis". Nielsen et al. (1978) conducted trapping studies in Oregon and Washington and developed a mixture of ODDA and ODDOH as a sex attractant for strawberry crown moth, Synanthedon bibionipennis (Boisduval), and a single ODDOH as an attractant for sequoia pitch moth, S. sequoiae (Hy. Edwards). A rather precise ratio of alcohol and acetate optimized trap captures of strawberry crown moth males. Although sequoia pitch moth males were captured in traps baited with E,Z-ODDOH and a mixture of Z,Z-ODDOH and E,Z-ODDA, Z,Z-ODDOH alone was the superior trap bait. We have received several reports (unpublished) from others that alcohols are important constituents of clearwing moth sex attractants.

Clearwing moth male trapping data accumulated and published throughout the world are summarized in table 1. If a species was attracted to more than 1 bait by an investigator, the bait resulting in most captures in comparative tests is given. In all cases, the bait included in table 1 can be considered adequate for monitoring seasonal emergence, but should not be considered to be the species' pheromone. Only lesser peachtree borer pheromone has been determined by isolation and through comparative trapping studies. However, attractants published for peachtree borer (Barry et al. 1978) and cottonwood crown borer (Underhill et al. 1978) may be close to the natural pheromone composition.

Clearwings for which sex attractants have not been published but which we have captured routinely are listed in table 2 along with the best attractant and states where they have been captured. Attractants were developed for the species of economic importance, including Paranthrene dollii and Sannina uroceriformis (Nielsen et al. unpublished). P. dollii was on the wing in early May in Oklahoma, and flight had collapsed by late June. S. uroceriformis began flying in Oklahoma in mid-June; we did not attempt to define its flight period. Albuna fraxini and Synanthedon rileyana are not economic pests but are interesting to us as some of the first clearwings to be attracted with alcohols. S. rileyana responded to fraction A from lesser peachtree borer female abdominal tips by hovering in the vicinity of this fraction. Apparently it was responding to alcohol which may be the long range attractant for this species. Perhaps E,Z-ODDA stimulates striking behavior which subsequently results in trap capture. Zenodoxus tineiformis (Esper), responded in numbers (> 30) to a trap baited with E,Z-ODDA and ignored a nearby trap baited with a commercial Z,Z-ODDA preparation containing minor amounts of other geometrical isomers. This is only the third species that has been reported to respond to pure E,Z-ODDA, the others being lesser

Table 1. Clearwing moth species for which sex attractants have been reported

Name	Host(s)	Attractant (ratio of isomers)	Reference ^{a/}
<u>Albuna fraxini</u>	<u>Parthenocissus quinquefolia</u> (Virginia creeper)	EZ-ODDA: ZZ-ODDOH (1:3)	3
<u>Carmentia bassiformis</u>	<u>Vernonia noveboracensis</u> (ironweed)	ZZ-ODDA: ZZ-ODDOH	1
<u>Carmentia texana</u>	<u>Eupatorium serotinum</u> <u>Artemisia</u> sp. and <u>Grindelia</u> sp.	ZZ-ODDA + other ODDA(s)	1
<u>Paranthrene asilipennis</u>	<u>Quercus</u> spp.	ZZ-ODDA + other ODDA(s)	1
<u>Paranthrene simulans</u>	<u>Quercus</u> spp.	ZZ-ODDA	2
<u>Paranthrene tabaniformis</u>	<u>Salix</u> spp. and <u>Populus</u> spp.	ZZ-ODDA: EZ-ODDOH (1:9)	3
<u>Podosesia aureocincta</u> (banded ash clearwing)	<u>Fraxinus</u> spp.	ZZ-ODDA + other ODDA(s)	1
		ZZ-ODDA: EZ-ODDA: ZZ-ODDOH (20:1:3)	3
<u>Podosesia syringae</u> (lilac borer)	<u>Syringa vulgaris</u> <u>Fraxinus</u> spp.	ZZ-ODDA	2
	<u>Ligustrum</u> spp. and <u>Chionanthus</u> spp.		
<u>Sesia tibialis</u> (cottonwood crown borer)	<u>Populus</u> spp.	ZZ-ODDA: ZZ-ODDOH (4:1)	11
<u>Synanthedon acerni</u> (maple callus borer)	<u>Acer</u> spp.	ZZ-ODDA: EZ-ODDOH (9:1)	3
<u>Synanthedon arkansasensis</u>	?	EZ-ODDA	1
<u>Synanthedon bibionipennis</u> (strawberry crown moth)	<u>Fragaria</u> spp.	EZ-ODDA: EZ-ODDOH (2:1)	6
<u>Synanthedon exitiosa</u> (peachtree borer)	<u>Prunus</u> spp.	ZZ-ODDA: EZ-ODDA (24:1)	5

Table 1. Clearwing moth species for which sex attractants have been reported--Continued

Name	Host(s)	Attractant (ratio of isomers)	Reference ^{a/}
<u>Synanthedon fatifera</u>	<u>Viburnum</u> spp.	ZZ-ODDA + other ODDA(s)	2, 3
<u>Synanthedon fulvipes</u>	<u>Alnus</u> spp.?	ZZ-ODDA + other ODDA(s)	3
<u>Synanthedon hector</u> (cherry tree borer)	<u>Prunus</u> spp.	ZZ-ODDA: EZ-ODDA (1:1)	7
<u>Synanthedon myopaeformis</u>	<u>Malus</u> spp.	ZZ-ODDA: EZ-ODDA (49:1)	9
<u>Synanthedon pictipes</u> (lesser peachtree borer)	<u>Prunus</u> spp.	EZ-ODDA	4
<u>Synanthedon rubrofascia</u>	<u>Nyssa</u> spp.	ZZ-ODDA: EZ-ODDA (3:1)	2
<u>Synanthedon sapygaeformis</u>	<u>Quercus</u> spp. galls	ZZ-ODDA + other ODDA(s)	1
<u>Synanthedon scitula</u> (dogwood borer)	Several unrelated woody plants	ZZ-ODDA	2, 10
<u>Synanthedon sequoiae</u> (sequoia pitch moth)	<u>Pinus</u> spp.	ZZ-ODDOH	6
<u>Synanthedon tenuis</u>	<u>Diospyros</u> spp.	ZZ-ODDA	8

^{a/} See numbered references in Literature Cited.

Table 2. Attractants useful for monitoring flight activity of selected clearwing species^{a/}

Species	Attractant (ratio)	Location(s)
<u>Albuna fraxini</u>	ZZ-OH	New York Ohio
<u>Paranthrene dollii</u>	EZ-OH: ZZ-OH (3:1)	Oklahoma
<u>Sannina uroceriformis</u>	EZ-OH: ZZ-OH (4:1)	Oklahoma
<u>Synanthedon rhododendri</u>	ZZ-A: EZ-A (49:1)	Ohio and Maryland
<u>Synanthedon rileyana</u>	EZ-OH: EZ-A (3:1)	Ohio and Georgia
<u>Zenodoxus tineiformis</u>	EZ-A	Dois Porto, Portugal

^{a/} Nielsen and Purrington (unpublished).

peachtree borer and Synanthedon arkansasensis Duckworth and Eichlin (Sharp et al, 1979).

We and others have captured single or a few specimens of several other clearwings, but these captures are not reported here since we do not consider the baits effective for survey or detection. However, Sharp (1979) reports such captures. This and similar information may be helpful to those who are trying to develop attractants for clearwings in the future.

Dutcher and All (1978) reported that squash vine borer male moths respond to calling female grape root borers. Consequently, we used EAG data from a male squash vine borer to guide our efforts in developing attractants for males of both species. Trapping studies were conducted in Virginia with the cooperation of P.B. Schultz, Virginia Truck and Ornamentals Research Station, Virginia Beach.

Most squash vine borer males were captured in traps baited with combinations of Z,Z- and E,Z-ODDA and Z,Z-ODDOH in approximately equal amounts. Grape root borer males were captured only in traps baited with a combination of Z,Z and E,Z alcohols or with a combination of Z,Z-ODDA and the two alcohols. However, we did not capture enough males of either species to conclude that the best baits were adequate for detection and survey. Consequently, we will continue our efforts to develop attractants for these species with cooperation of researchers in several southern states.

At this time, attractants are known for males of most clearwings of economic importance in the United States. However, little pheromone chemistry

has been done with the Sesiidae. Following the Tumlinson et al. (1974) paper, and armed with the knowledge that cross attraction occurs in the Sesiidae, entomologists began evaluating isomers of ODDA and ODDOH and isomeric mixtures as clearwing attractants. The astonishing success in these ventures and the lack of significant financial support for clearwing moth research apparently quelled interest in further pheromone chemistry studies with this group.

Even though we have good EAG data for squash vine borer we were unable to develop a suitable sex attractant for this species. This failure combined with clearwing moth EAG results with Z,Z-aldehyde and analogs may indicate that some clearwings use chemicals other than Z,Z-and/or E,Z-ODDAs and ODDOHs in their sex pheromones.

We believe the most efficient and rational way to further our knowledge of clearwing moth sex attraction is through further pheromone chemistry research. Perhaps those of us interested in this group of remarkable moths can combine our efforts to generate funding necessary to attack this problem.

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DISRUPTION OF MATING COMMUNICATION IN PEACH BORERS

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The sex pheromones of moths have demonstrated feasible roles in modern orchard management, primarily as tools in pest control decision making (Rock et al. 1978, Wearing and Charles 1978). Nielsen (1978) presents a method for coordinating spray programs for sesiids in nurseries with sex pheromone traps, and Yonce et al. (1977) and Gentry et al. (1978) have demonstrated that captures of male sesiid peach borers in pheromone traps accurately portray population cycles. Mass trapping of males with sex pheromones has apparently suppressed populations of some orchard and vineyard Lepidoptera (Hagley 1978, Roelofs et al. 1976), and Wong et al. (1972) and Voerman et al. (1978) found that sex pheromone traps will capture a high percentage of the male sesiids that emerge in an area. Mass trapping is not developed commercially to control sesiids or other orchard Lepidoptera.

The above uses of synthetic sex pheromones attempt to maximize the response of male moths. This report will present a method of exploiting sex pheromones with an opposite goal.

PRINCIPLES OF MATING DISRUPTION

Atmospheric permeation with a synthetic female sex pheromone is a method of disrupting the mating communication process first discussed by Beroza in 1960 (Beroza 1976). His hypothesis was if a synthetic sex pheromone were emitted from many dispersed particles, the males that respond to the pheromone would be unable to distinguish between the synthetic odor and that of the relatively few females present in the same area; thus, no mating would occur. This became known as the "confusion" technique, and the implied mechanism of effect is that of disorientation or misdirection of males in the presence of a large number of pseudofemales (Beroza 1976). Research with the cabbage looper, *Trichoplusia ni* (Hübner), established the feasibility of disrupting sex pheromone communication by distributing synthetic pheromone over cabbage fields (Gaston et al. 1967, Shorey et al. 1967). These scientists also realized that sensory thresholds must be affected in the presence of physiologically large amounts of omnipresent pheromone and hypothesized that sensory adaptation and/or habituation would be the primary mechanism(s) of effect. In any case where a pheromone or a parapheromone that elicits anemotaxis in males is used as the "disruptant," all of the proposed mechanisms of effect would contribute to the failure of a male to locate a mate (Shorey

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et al. 1976). Many nonattractive chemicals (do not cause sexual excitation and/or do not cause anemotaxis) are effective disruptants (Shorey 1977); thus, disorientation or confusion effects are not crucial to blocking mating communication.

Roelofs (1978) presents convincing evidence that the most effective disruptant of sex pheromone communication in Lepidoptera is a chemical or chemical blend that closely approximates the sex pheromone of the target species. The female sex pheromone of the lesser peachtree borer, Synanthedon pictipes (Grote and Robinson), is (E,Z)-3,13-octadecadien-1-ol acetate (EZODDA). The Z,Z isomer of this chemical is a pheromone constituent of the female peachtree borer, Synanthedon exitiosa (Say), (Tumlinson et al. 1974). Tumlinson et al. (1974) found that as little as 0.5% of the Z,Z isomer admixed with EZODDA inhibited the close range response of male lesser borers. Barry et al. (1978) determined that even though peachtree borer males are strongly attracted by very pure ZZODDA, they are not readily captured in traps baited with this isomer. Maximum trap capture of peachtree borer males is achieved with mixtures of ZZ- and EZODDA ranging from 98:2 to 92:8.

MATING DISRUPTION EXPERIMENTS

During the summer of 1974, McLaughlin and coworkers began mating disruption experiments using the synthetic peach borer pheromones. The methods were those commonly used to evaluate the disruptive potential of a chemical. Traps baited with either virgin female moths or with synthetic pheromones were placed in peach trees and some of these traps were surrounded with various densities of evaporators that released the test materials into the atmosphere. The number of males captured in traps in untreated areas of peach orchards were compared to those in the traps within pheromone-permeated areas, the rationale being that any reduction in trap capture caused by the treatment is related in some manner to the success in attracting a mate of a female in the same environment. Mitchell et al. (1976) determined with Heliothis zea (Boddie), H. virescens (F.), and Spodoptera frugiperda (J. E. Smith) that female-baited traps are an accurate indicator of the effect that a disruptant has on mating in the field.

McLaughlin et al. (1976) reported that both of the pheromonal ODDA isomers are effective disruptants of mating communication in the lesser peachtree borer or the peachtree borer. They did not determine the amount of each chemical required in the air to achieve disruption. Subsequently, quantification of some slow-release formulations of EZ- and ZZODDA (Conrel hollow fibers and Hercon plastic laminates) was accomplished (J. H. Cross et al., Insect Attractants and Basic Biology Research Laboratory, Abstract No. 10, 176th National American Chemical Society Meeting, Division of Pesticide Chemistry, September 11, 1978, Miami Beach, FL) and in 1977 these formulations were hung from peach trees in 400 m² plots. The disruptive effects were measured with synthetic pheromone-baited traps. Procedures were as described in McLaughlin et al. (1976). The amount of synthetic sex pheromone required to prevent males from being captured in these traps (table 1) was 10 to 100 times

less than that required to disrupt sex pheromone communication in most Lepidoptera (Rothschild 1975). The peach borer pheromones are less volatile than other lepidopteran pheromones, most of which are similar materials of 12- to 16-carbon atoms (Mayer and McLaughlin 1975), and the borers may require less pheromone in the atmosphere to elicit a behavioral response than other Lepidoptera. Thus, peach borer males would be inhibited in detecting the pheromone produced by females by relatively low levels of omnipresent synthetic pheromone.

Table 1.--Disruption of sex pheromone communication in lesser peachtree borer (LPTB) and peachtree borer (PTB) by permeation of the air surrounding synthetic-pheromone-baited traps with isomers of 3,13-octadecadien-1-ol acetate

Isomer	Ratio	Rate of permeation mg evaporated/ha/h	Species	% Disruption + SE
<u>E,Z</u>	-	.03	LPTB	61 + 5
<u>E,Z</u>	-	.15	LPTB	100 + 0
<u>Z,Z</u>	-	.03	LPTB	77 + 4
<u>Z,Z</u>	-	.15	LPTB	99 + 1
<u>E,Z</u>	-	.03	PTB	95 + 5
<u>E,Z</u>	-	.15	PTB	100 + 0
<u>Z,Z</u>	-	.03	PTB	87 + 8
<u>Z,Z</u>	-	.15	PTB	100 + 0
<u>Z,Z:E,Z</u>	96:4	.03	PTB	99 + 1
<u>Z,Z:E,Z</u>	96:4	.15	PTB	100 + 0

Sex pheromone communication in the peachtree borer appears to be disrupted by lesser quantities of ODDA isomers than are required to disrupt the lesser peachtree borer (table 1, McLaughlin et al. 1976). McLaughlin et al. (1972, 1976) determined that sex pheromone communication in Lepidoptera is most effectively disrupted when the permeating chemical is evaporated at or above the height at which sexually active males tend to fly. Lesser peachtree borer males are more readily captured in pheromone traps placed above the mid-height of peach trees and peachtree borer males are trapped in greatest numbers when traps are below mid-tree height (table 2). This preferred flight or pheromone response height in relation to the tree agrees with the oviposition site and larval habitat of each species. Lesser borers attack peach trees above the ground line, preferring wounds as oviposition and entry sites, and peachtree borer larvae occur only at the ground line of the trunk or below (Girault 1907, King 1917).

Table 2.--Effect of height of pheromone trap placement in peach trees on capture of male lesser peachtree borer (LPTB) and peachtree borer (PTB)^{1/}

Trap elevation in tree	$\bar{X} \pm \text{SE males/trap/day}$ ^{2/}	
	LPTB	PTB
Top (ca. 3 m)	4.4 \pm 0.7 a	0.4 \pm 0.1 a
Middle (ca. 1.5 m)	2.6 \pm 0.6 b	3.7 \pm 1.1 b
Lower (ca. 0.3 m)	2.3 \pm 0.5 b	5.4 \pm 1.7 c

^{1/} Experimental design and LPTB data in McLaughlin et al. (1976).

^{2/} Means in a column followed by unlike letters are statistically different. Duncan's NMR (P = 0.05).

CONCLUSIONS

The future of insect sex pheromones, particularly those of the Lepidoptera, as important elements in orchard pest management seems bright. Pheromones have proven effective in the detection of orchard moths and can be fine tuned as predictive devices. Their future as direct control agents is less clear. Air permeation studies with four tortricid orchard and vineyard species have demonstrated that crop protection is feasible (Taschenberg et al. 1974, Rothschild 1975, Arn et al. 1976, Taschenberg and Roelofs 1976, Minks et al. 1976). However, these tortricid species are of critical importance only when the crop is fruiting, and economic control is obtained in many cases by suppression of the 1st generation. The lesser peachtree borer is present in orchards each season from soon after the last frost in spring until the first in the fall or winter. This is a very long period for pest suppression with a technique such as air permeation which must be in place and effective during all mating flights. Pheromone traps provide the once lacking means to monitor and even predict (Gentry et al. 1978) peak flights of this species and may eventually allow us to make applications of mating disruptants and/or pesticides very effectively. The peachtree borer has a more restricted flight period in the latter half to one-fourth of the season, and is more likely to be controlled by air permeation with synthetic sex pheromone.

My own observations and those of other workers (Girault 1907, King 1917) indicate that both lesser and peachtree borer females mate soon after emergence and at or very near the site of emergence. Females of both species also decline in their ability to attract males if not mated soon after eclosion and both species will begin to lay infertile eggs if left unmated (Cory 1913, Cleveland et al. 1968, Wong et al. 1969). These attributes would make each species vulnerable to mating disruption.

Several technical means are available to test the effectiveness of air permeation with synthetic sex pheromone to disrupt mating in sesiid peach borers. Two companies in particular are pursuing this method for the control of Lepidoptera, Conrel, a subsidiary of Albany International, and the Hercon Group, Herculite Products, Inc., a subsidiary of Health-Chem Corporation. Conrel manufactures a hollow fiber controlled release vapor dispensing system, while the Hercon system is a polymeric laminate (Rothschild 1979). These products have been tested by myself and by C. R. Gentry and C. E. Yonce at the Southeastern Fruit and Tree Nut Research Laboratory, SEA/AR, USDA, Byron, Ga. (personal communication). Both systems appear to be satisfactory slow-release devices for the sesiid pheromones. Because of its more ready availability, ZZODDA is the disruptant of choice in these formulations.

Tests thus far, such as the quantification and height experiments described earlier in this paper, have used only the station approach for distributing these formulations. Usually 20- to 50-fiber packets or 1-in² laminates were hung individually at various spacings from trees in the orchard. A 2-year test in one Georgia peach orchard indicates that this approach will suppress the peachtree borer (C. E. Yonce, personal communication). This labor intensive approach to placing the pheromone evaporators seems practical as workers pass through orchards frequently at present and the evaporators would not interfere with other cultural practices or with harvesting. This approach also avoids contamination of the fruit with the formulation. Both companies have developed broadcast formulations that could be applied from ground or air equipment. C. R. Gentry has informed me that he will test these formulations in Georgia during the summer of 1979.

In conclusion I must emphasize that pheromones and other behavior-modifying chemicals do not promise a total answer to any pest control need, certainly not to the control of peach borers. Pheromones do promise to be a powerful weapon in our arsenal of pest control agents. They are weapons we have yet to learn to use. If they can be developed as direct control agents, pheromones can serve to reduce our reliance on conventional pesticides. Even more exciting is the prospect that reduction in pesticide levels in orchards can lead to the development of biological control techniques, not only for the borers, but for other pests of peach trees.

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DISTRIBUTION AND SEASONAL OCCURRENCE OF SESIIDAE (LEPIDOPTERA)
ATTRACTED TO E,Z AND Z,Z ACETATE AND ALCOHOL

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The major components of the sex pheromone systems of the lesser peachtree borer, Synanthedon pictipes (Grote and Robinson), and the peachtree borer, Synanthedon exitiosa (Say), are, respectively, the E,Z and Z,Z isomers of 3,13-octadecadien-1-ol acetate (EZA and ZZA) (Tumlinson et al. 1974). Soon after the two pheromones were made available it became evident that at least 95% ZZA, in a mixture containing very small amounts of the other stereoisomers (2-3% EZA, and 1% EEA and ZEA), effectively attracted males of various sesiids (see table 1). This finding prompted additional research throughout the United States. Many species of sesiids were captured, and, in a short time, males were captured that represented the entire phylogenetic range of the Sesiidae. This paper reports on trapping studies conducted in Florida and in the Western United States and Mexico.

In the western United States and Mexico, a pheromone blend (95% ZZA, 2-3% EZA, and 1% EEA and ZEA) prepared by Farchan Division, Storey Chemical Co., Willoughby, Ohio, was used as bait in surveys conducted since 1974. Several traps designed to capture live specimens were used with varying degrees of success depending on the design, location of the traps, and behavior of the males attracted to the traps. Some males were captured in baited Malaise traps; however, most males were captured when the attractant was attached to the handle or to the cloth material near the open end of a collecting net. Thus, the collector could move around freely and stop frequently to sample different select habitats, since the male moths would fly directly to the source of the attractant.

The procedures used to capture male sesiids in Alachua, Marion, and Broward Counties (Florida) are published (Sharp et al. 1978a, b). The attractants listed in table 1 were used singly or in various combinations as bait. Captures of males varied from year to year depending on the life cycles, location, number of traps, weather, attractants used, etc.

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WESTERN UNITED STATES AND MEXICO

The following list and summary contain selected species of Sesiidae and were prepared from specimens captured in the Western United States and Mexico. Specific collecting locals and generally known distributions are given. Additional species of Alcathoe Hy. Edwards, Carmenta Edwards, and Saphona Walker were captured; however, several of those from Mexico were omitted because their taxonomic status is in doubt.

Alcathoe pepsoides Englehardt--New Mexico: San Miguel Co., 3.2 km N Pecos, July 1977. Distribution: Utah, Colorado, Arizona, New Mexico and western Texas.

Carmenta albociliata Englehardt--Mexico: Nuevo Leon, 29.0 km W Linares, Sept. 1975; Texas: Uvalde Co., 4.8 km N Uvalde, May 1977. Distribution: Previously known only from central Texas; range extended to Nuevo Leon, Mexico.

Carmenta armasata (Druce)--Mexico: Nuevo Leon, 29.0 km W Linares, Sept. 1975. Distribution: Previously known only from type-locality, Durango, Mexico.

Table 1.--Chemical attractants used to determine the distribution and seasonal occurrence of sesiids in the Western U.S., Mexico, and Florida^{1/}

E,Z-3,13-Octadecadien-1-ol acetate, 99% pure. (EZA)

Z,Z-3,13-Octadecadien-1-ol acetate, 99% pure. (ZZA)

E,Z-3,13-Octadecadien-1-ol, 99% pure. (EZH)

Z,Z-3,13-Octadecadien-1-ol, 99% pure. (ZZH)

1974 Farchan Z,Z-ODDA: 80.0% ZZ
 5.6% ZE
 4.2% EZ
 1.3% EE

1975 Farchan Z,Z-ODDA: 95.0% ZZ
 2.2% ZE
 1.6% EZ
 0.6% EE

Z,Z-ODDA (H-combination): 96.0% ZZ
 1.9% ZE
 1.3% EZ
 0.6% EE

^{1/} Analyses provided by J. H. Tumlinson, Research Leader, Insect Chemistry Group, Insect Attractants, Behavior, and Basic Biology Research Laboratory, USDA, SEA/AR, Gainesville, FL.

Carmenta hipsides (Druce)--Mexico: Nuevo Leon, 29.0 km W Linares, Sept. 1975; Hidalgo, 22.5 km S Jacala, Sept. 1975; Puebla, 9.6 km N Chapulco, Oct. 1975; Michoacan, 14.5 km W Morelia, Oct. 1975. Distribution: Described from Amula, Guerrero, Mexico; extends range north to Nuevo Leon.

Carmenta mimuli (Hy. Edwards)--New Mexico: Roosevelt Co., 11.3 km NE Portales, July 1977; Mexico: Chihuahua, 25.7 km NW Meoqui and 8 km NE Saltaices, Aug. 1976; Coahuila, 32.2 km N Saltillo, 27.4 km SE Saltillo, 1.6 km SE Saltillo, 14.5 km W Los Lirios, Sept. 1976, 1977; Nuevo Leon, 8.0 km W Dr. Arroyo, 16.1 km NW Providencia, Sept. 1976; Zacatecas, 3.2 km SE Fresnillo, Sept. 1977; San Luis Potosi, 4.8 km W Cedral, 33.0 km NW San Luis Potosi, Sept. 1976, 1977; Puebla, 7 km SE Morelos, 9.6 km S Zapotitlan, Oct. 1975; Oaxaca, 3.2 km S Puebla-Oaxaca state line, Oct. 1975, 16 km NW Oaxaca, 11.4 km N Yanhuitlan, Sept. 1976; Hidalgo, 4.8 km N Zimapan, Sept. 1975; Jalisco, 4.2 km NW Tequila, Sept. 1976; Durango, 25.7 km NW Bermejillo, Sept. 1976. Distribution: Previously known from a few scattered records from North Dakota, Colorado, New Mexico, Arizona, and western Texas; extends range over much of Mexico.

Carmenta pallene (Druce)--Arizona: 8.0 km W Portal, Malaise trap with pheromone, Aug. 1978; Mexico: Vera Cruz, 9.6 km SE Rinconada, Malaise trap with pheromone, Sept. 1975. Distribution: Previously known only from Tabasco, Mexico; extends range to southeastern Arizona.

Carmenta tecta (Hy. Edwards)--Arizona: Pima Co., Kit Peak, live trap with pheromone, Aug. 1974. Distribution: Arizona, New Mexico, and Texas.

Carmenta welchellorum Duckworth and Eichlin--Described from specimens collected in Malaise trap with pheromone. Texas: Uvalde Co., 4.8 km N Uvalde, May 1977.

Euhagena emphytiformis (Walker)--New Mexico: Grant Co., Silver City, July 1977; Mexico: Coahuila, 35.4 km W Zaragosa, Sept. 1976. Distribution: Southeastern United States, Nebraska, Colorado, New Mexico, and Arizona; extends range to northern Mexico.

Melittia calabaza Duckworth and Eichlin--Only species in this genus and complex of squash vine borers to have shown an attraction to the pheromones used. Collected with pheromones in central Texas and western Mexico. Distribution: Arizona, Texas, widely throughout Mexico except for east coast and central plateau.

Paranthrene fenestrata Barnes and Lindsey--New Mexico: Sierra Co., Emory Pass, July 1977; Mexico: Hidalgo, 13 km NE Jacala, 26 km S Jacala, June and July 1977. Distribution: Previously known only from the female types from Cochise Co., Arizona; range extended to New Mexico and eastern Mexico; males discovered for the first time; new color form also attracted to pheromone at New Mexico locality.

Pennisetia eucheripennis (Boisduval)--Mexico: Vera Cruz, 8.0 km S Las Vigas, Sept. 1975; Oaxaca, 40 km S Valle Nacional, July 1977. Distribution: Previously known only from type; specific locality in Mexico unknown.

Penstemonia clarkei Englehardt--Idaho: Boise Co., 8.0 km W Idaho City, July 1977. Distribution: Montana, Idaho, Washington south to California. Additional specimens have been captured with the pheromone in several localities in northern California. Specimens taken in the high passes in the Sierra Nevada may represent an undescribed species.

Sesia tibialis (Harris)--Collected with pheromone at many locations in California, Idaho, and New Mexico. Distribution: Nova Scotia and New England, west to Vancouver, British Columbia; Rocky Mountains of Wyoming, Colorado, and New Mexico, west to the Pacific Coast.

Synanthedon albicornis (Hy. Edwards)--California: Sacramento, June, July 1975; San Joaquin Co., Lodi, July 1975. Distribution: California and Nevada, north to British Columbia and Northwest Territory.

Zenodoxus heucherae Hy. Edwards--California: Alpine Co., 3.2 km E Ebbetts Pass, Aug. 1978. Distribution: Sierra Nevada of California from Modoc Co. to Tuolumne Co.

Zenodoxus mexicanus Beutenmuller--Texas: Big Bend, Santa Elena Canyon, Aug. 1975. Distribution: Wyoming, Colorado, and Texas.

Zenodoxus rubens "bexari" Englehardt--Texas: Val Verde Co., Del Rio, Oct. 1976; Mexico: Coahuila, 32.2 km N and 1.6 km SE Saltillo; Nuevo Leon, 6.4 km W Iturbide, 8.0 km W Dr. Arroyo, 22.5 km S San Juanito; Tamaulipas, 6.4 km and 24.1 km NE Jaumave; San Luis Potosi, 9.7 km E Matehuala, Sept. and Oct. 1975, 1976. Distribution: Arizona, New Mexico, and Texas; extends range into eastern Mexico.

FLORIDA

Currently there are 32 recognized species of Sesiidae in Florida (Sharp et al. 1978a), and 21 of them were captured in baited Pherocon sticky traps during 1975-78. A brief discussion of the sesiids follows and includes the best attractant(s) for each. Figures of seasonal occurrence for particular species are presented when significant numbers of males were captured.

Paranthrene dollii (Neumoegen)--Males were captured near Lowell and Belleview during Apr. 24-Dec. 1, 1977 (except Aug.). Of all the males captured, 22 (41%) were captured in traps baited with a 50-50% mixture of EZH:ZZH. Fewer numbers of males were captured in traps baited with other attractants. In 1978 a male was captured on June 9.

Paranthrene asilipennis (Boisduval)--Males were captured only in Mar. near Hawthorne and Pedro in traps baited with 1975 ZZA (table 1).

Paranthrene simulans palmii (Hy. Edwards)--This was the most frequently captured species of the genus. Males displayed 2 flight periods that perhaps represent 2 generations (fig. 1). During Apr. 4-July 15, 1977, near Lowell, 56 males (53%) were captured in a trap baited with 1975 ZZA; during Apr. 1-Sept. 20, 1978, 30 males (80%) were captured in 8 traps baited with different mixtures of ZZA:EZA:ZZH; during Apr. 21-Sept. 20, 1978, 13 males (57%) were captured in a trap baited with ZZA:EZA:EZH (2000:200:200 μ g) compared to 8 males (35%) captured in 2 traps baited with different mixtures of ZZA:EZH.

Vitacea polistiformis seminole (Neumoegen)--Males were never captured in baited traps in Alachua or Marion Counties. A male was captured in Miramar (Broward Co.) on July 2, 1978, in a trap baited with 2000 μ g of EZA. Three additional males were captured there on Sept. 4, 1978, in a trap baited with 1974 ZZA. The usual months of occurrence for the species are July and Aug. (Englehardt 1946).

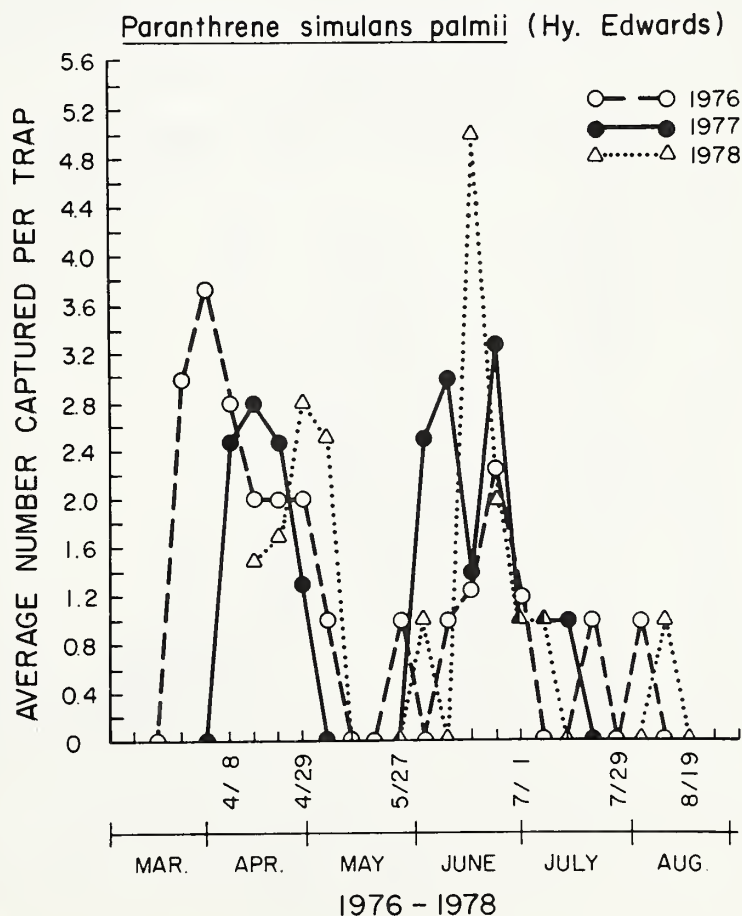


Figure 1.--Seasonal occurrence in north central Florida of males of Paranthrene simulans palmii (Hy. Edwards).

Vitacea scepsiformis (Hy. Edwards)--Males have been captured frequently from May-Oct. (fig. 2). During May 19-Oct. 6, 1977 near Lowell, 184 males (44%) were captured in 4 traps baited with different mixtures of ZZA:EZA; 98 males (24%) were captured in a trap baited with 1974 ZZA; 39 males (10%) were captured in a trap baited with 1975 ZZA; and 38 males (10%) were captured in a trap baited with EZA. Fewer males were captured in 1978 (17 in July, 31 in Aug. and 19 in Sept.).

Synanthedon alleri (Englehardt)--Males were captured near Hawthorne from July - Dec. 22, 1975 in traps baited with EZA. In 1976, males were captured most often in Jan. but rarely from Feb.-Apr. None were captured in 1976 after Apr. until the period, Aug. 3-Nov. 2, when 38 males (78%) were captured in 3 traps baited with different mixtures of EZA:EZH.

Synanthedon arkansasensis Duckworth and Eichlin--This species was previously reported in Florida from the panhandle area (Duckworth and Eichlin 1973). It was frequently captured in Gainesville in 1975, a peak number of 148 males being captured in Sept. The best attractant was EZA. Sparse captures of males (<10) in traps baited with EZA or EZH:ZZH from 1976-78 probably indicate that the moths have a 2-3 year life cycle.

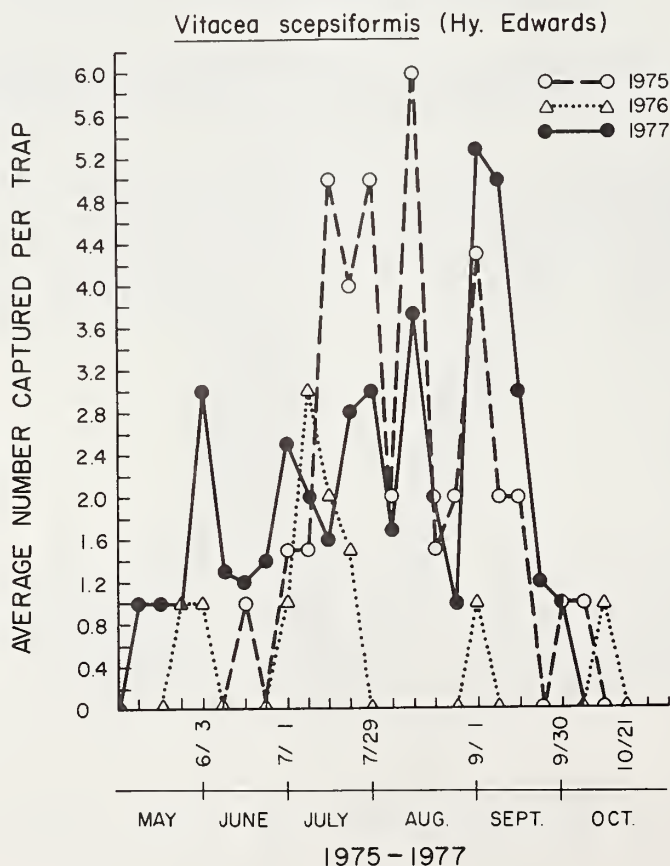


Figure 2.--Seasonal occurrence in north central Florida of males of Vitacea scepsiformis (Hy. Edwards).

Synanthedon decipiens (Hy. Edwards)--Englehardt (1946) first reported the species from Pensacola, Fla. Fewer than 10 males were captured in traps baited with 1974 ZZA in Alachua Co. in July and Aug. 1975-77. In Sept. 1978, only 2 males were captured and they were in a trap baited with EZA.

Synanthedon fatifera Hodges--A male was captured near Hawthorne on May 13, 1977 in a trap baited with 1975 ZZA.

Synanthedon geliformis (Walker)--Males were captured during Apr.-Dec. 1977 (fig. 3). Attractants having high percentages of ZZA were good attractants.

Synanthedon pictipes (Grote and Robinson)--Males fly throughout the year (Sharp et al. 1978b). Near Lowell during Apr. 6-24, 1978, 181 males (89%) were captured in a trap baited with 2000 μ g of EZA. During Apr. 26-May 12, 1978, 72 males (66%) were captured in 2 traps baited with different mixtures of EZA:EZH compared to 20 males (18%) captured in a trap baited with EZA (2000 μ g) and to 15 males (14%) captured in a trap baited with ZZA:EZA:EZH (200:2000:200 μ g). During Sept. 20-Nov. 20, 1978, 4 males (49%) were captured in a trap baited with a 50-50% mixture of EZA:EZH, and 45 males (47%) were captured in 2 traps baited with different mixtures of EZA:ZZA.

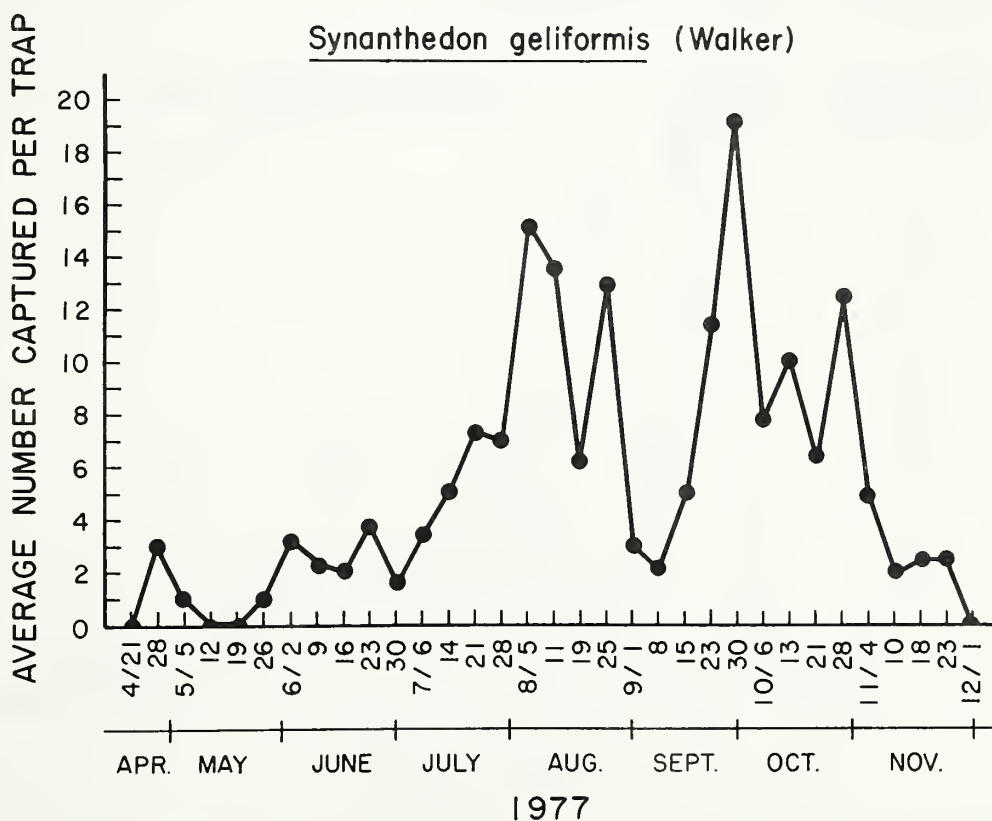


Figure 3.--Seasonal occurrence in north central Florida of males of Synanthedon geliformis (Walker)

Synanthedon exitiosa (Say)--Males have one major flight period (Sharp et al. 1978b). During 1978, males were captured during July-Oct. with a peak number captured in Aug. The best attractant is a mixture of ZZA:EZA (96:4) (Barry et al. 1978).

Synanthedon rubrofascia (Hy. Edwards)--Males were captured in about equal numbers between Apr. 1 and Aug. 19, 1976. They have rarely been captured since that time. Good attractants were H-combination ZZA and 1975 ZZA.

Synanthedon sapygaeformis (Walker)--Males were frequently captured in traps baited with high percentages of ZZA as 1975 ZZA but were also attracted to almost every attractant used. Males were captured in large numbers from Feb.-Dec. with peak captures in Mar. and Apr. (fig. 4).

Podosesia syringae (Harris)--Nielsen and Purrington (1974) first reported the species in Florida. Males usually begin flying in the field in Feb. and are very abundant during Mar. (figs. 5a, 5b). The start of the flight of P. syringae was missed in 1978 because baited traps were not set out until Apr.; however, the last male was captured on May 5. During Mar. 18-Dec. 9, 1978, near Lowell, 223 (94%) males were captured in a trap baited with 1975 ZZA. Nielsen and Purrington (1978) reported that pure ZZA was an effective attractant. Pure ZZA received by us from F. F. Purrington (OARDC, Wooster, Ohio) was tested in the field at several locations and was not effective.

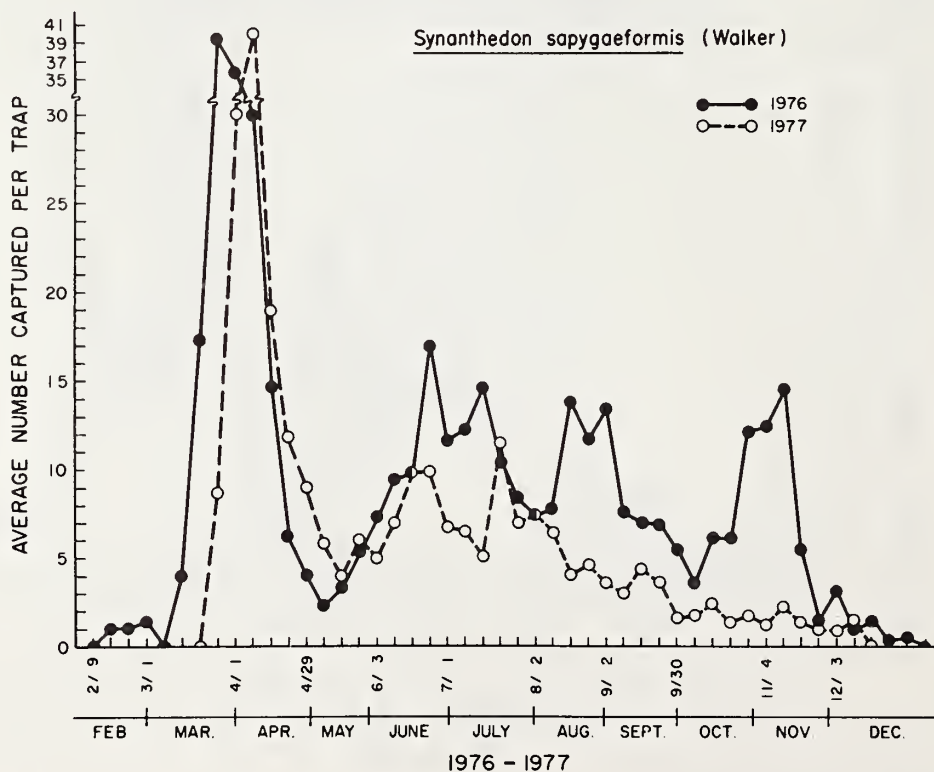


Figure 4.--Seasonal occurrence in north central Florida of males of Synanthedon sapygaeformis (Walker)

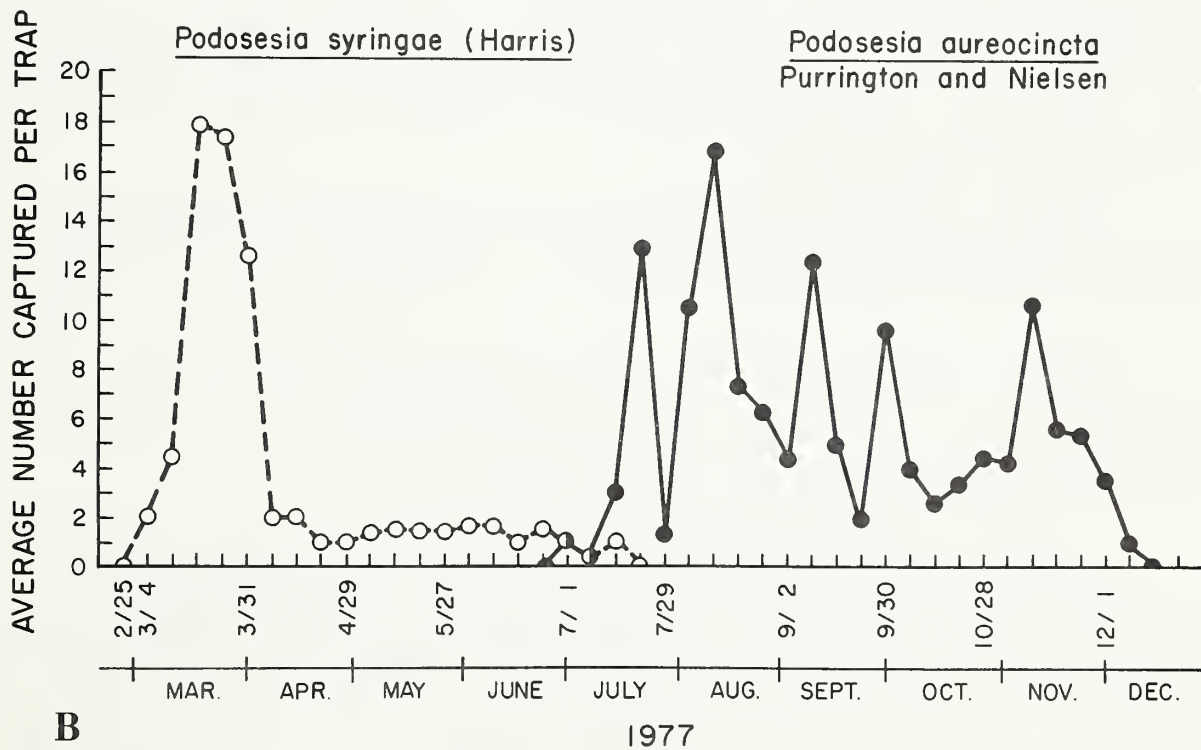
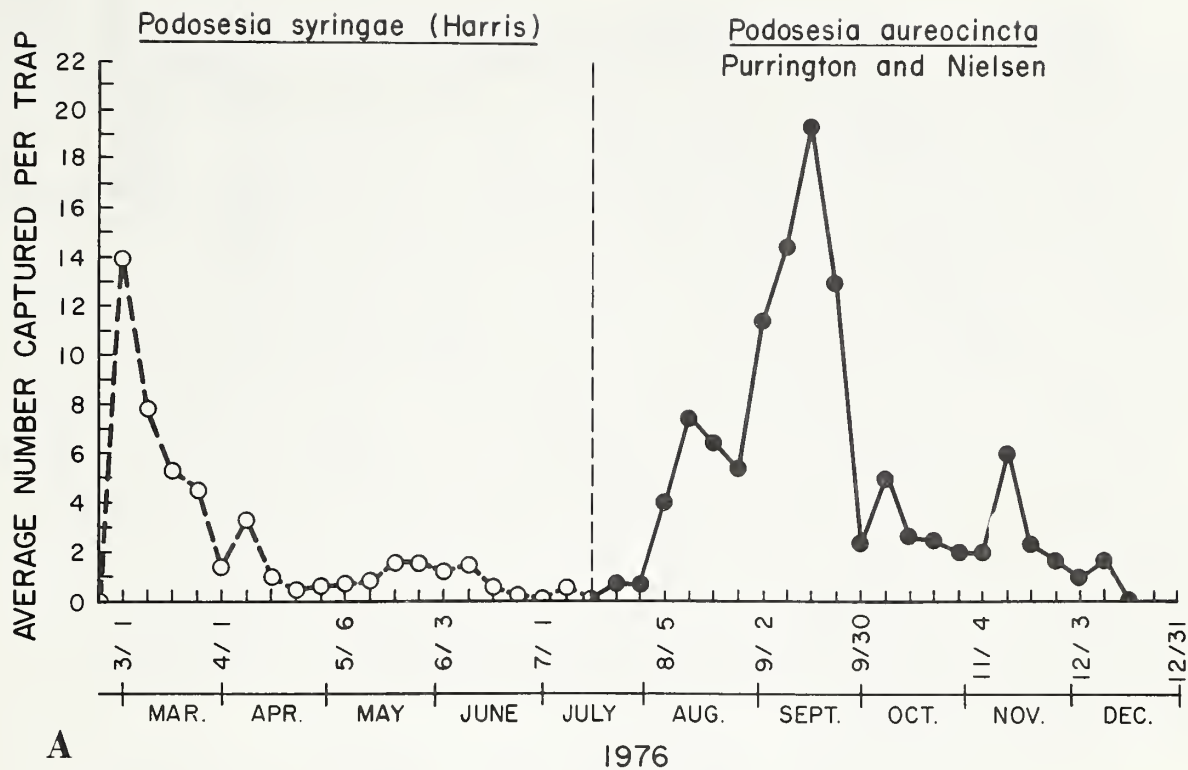


Figure 5.--Seasonal occurrence in north central Florida of males of Podosesia syringae (Harris) and P. aureocincta Purrington and Nielsen for (a) 1976 and (b) 1977.

Podosesia aureocincta Purrington and Nielsen--The species was reported from Florida by Purrington and Nielsen (1977). Usually males were trapped from July-Dec. (figs. 5a, 5b). Males were captured from July 10-Oct. 6, 1978, and a peak number of was were captured in Aug. near Lowell. The flight in 1978 ended almost 2 months earlier than previously reported, probably due to the unusual lack of precipitation during Aug.-Nov. During Mar. 18-Dec. 9, 1977, near Lowell, 347 (64%) of the P. aureocincta males were captured in a trap baited with 1975 ZZA. Other good attractants included different mixtures of ZZA:ZZH and a 50-50% mixture of ZZA:EZH. Nielsen and Purrington (1978) reported that a 20:1:3 mixture of ZZA:EZA:ZZH was effective for attracting the males. We tested this blend and a 20:1:4 mixture. Neither were effective attractants. For example, between Apr. 7 and Sept. 20, 1978, near Lowell, 7 (39%) P. aureocincta males were captured in a trap baited with EZH (200 μ g), and 7 (39%) were captured in a trap baited with 1975 ZZA. No males were captured in traps baited with ZZA (200 μ g) or with a 20:1:4 mixture of ZZA:EZA:ZZH. During Apr. 26-Sept. 20, 1978, near Lowell, 19 (40%) males were captured in a trap baited with a 50-50% mixture of ZZA:EZH, 13 (28%) were captured in a trap baited with ZZA:EZA:EZH (2000: 200:200 μ g), 11 (23%) males were captured in a trap baited with a 50-50% mixture of EZA:EZH, and 4 (9%) were captured in a trap baited with ZZA:EZH (200:200 μ g).

Sannina uroceriformis Walker--Males were frequently captured in 1976 and 1977 (fig. 6) >98% being captured in traps baited with at least 500 μ g of EZH. During Apr. 7-Sept. 20, 1978, near Lowell, 15 males (100%) were captured in traps baited with EZH (2000 μ g). Between Apr. 26 and Sept. 20, 1978, in the same area, 26 males (93%) were captured in a trap baited with a 50-50% mixture of ZZA:EZH; fewer males were captured in traps baited with EZA.

Carmenta bassiformis (Walker)--Males were captured in about equal numbers during June-Aug. 1977, and the best attractants were different mixtures of ZZA:ZZH and 1975 ZZA.

Carmenta suffusata Englehardt--A male of this rare species was captured on June 7, 1976, near Lowell in a trap baited with EZH (500 μ g). Two males were captured there again (one each) on June 7 and 9, 1978, both in a trap baited with ZZA:EZH (2000:2000 μ g). Previously, only a total of 3 males were known from Kansas and Oklahoma.

Carmenta texana (Hy. Edwards)--Males were captured from Apr.-July (peak in June) and Aug.-Nov. (peak in Sept.) during 1975-76. In 1977 males were captured less often during Apr.-Aug. None were captured in 1978 in north central Florida; however, a male was captured Sept. 9, 1978, in Miramar, Fla., in a trap baited with 1974 ZZA. The best attractant was 1975 ZZA.

Alcathoe carolinensis Englehardt--A male of this rare species was captured near Lowell on Oct. 6, 1977 in a trap baited with EZA:ZZA (1500:500 μ g). None was captured in 1978 using the same mixture.

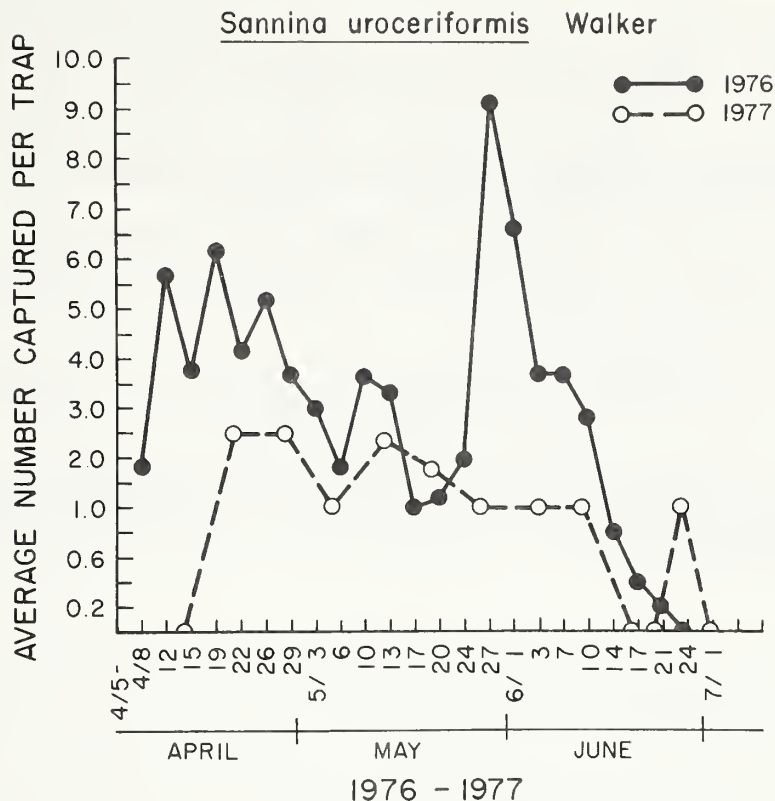


Figure 6.--Seasonal occurrence in north central Florida of males of Sannina uroceriformis Walker

In conclusion, the pheromones and various attractants have proven to be remarkable survey tools, adding greatly to our knowledge of species diversity, distribution, and general habitat preferences after just a few years of active, fairly random sampling. Many species that were thought to be rare have been found to be rather common, and many species captured are new to science.

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TRAPPING AND BIOLOGY OF PODOSESIA AND PARANTHRENE BORERS

J. D. Solomon^{1/}

INTRODUCTION

Larvae of the family Sesiidae are borers in trunks, bark, stems, and roots of trees, shrubs, vines, and other plants. The genera Podosesia and Paranthrene contain some of the species most damaging to economically important hardwood trees.

Recent work by Nielsen et al. (1975) and Tumlinson et al. (1974) on sex attractants of Sesiidae appeared applicable to Podosesia and Paranthrene. Therefore, samples of the synthetic attractants were obtained to help clarify borer biologies at Stoneville, Miss. This paper is devoted largely to Podosesia syringae (Harris), Podosesia aureocincta Purrington and Nielsen, Paranthrene simulans Grote, and Paranthrene tabaniformis (Rottemburg). The importance and biology of these species are summarized, and trapping studies, as they relate to abundance, seasonal activity, and diel periodicity of flight, are presented.

BIOLOGY AND IMPORTANCE

Podosesia syringae, a univoltine species with adult emergence from February through July (Purrington and Nielsen 1977), damages ash (Fraxinus spp.), lilac (Syringa spp.), and other trees and shrubs in the family Oleaceae. Green ash is receiving attention by foresters as a species suitable for artificial regeneration. But, it has been seriously damaged by P. syringae whether grown for timber in the South (Roberts 1956), for shelterbelts in the Great Plains (Dix et al. 1978), or for shade and ornamental purposes in Canada and elsewhere (Peterson 1964). In northeast Ohio, damage to lilac in nurseries has been estimated at \$5,000 per acre per cropping cycle (Nielsen and Balderston 1973).

^{1/}Stationed at the Southern Hardwoods Laboratory, which is maintained at Stoneville, Miss., by the Southern Forest Experiment Station, Forest Service--USDA, in cooperation with the Mississippi Agricultural and Forestry Experiment Station and the Southern Hardwood Forest Research Group.

Podosesia aureocincta, a univoltine species with adult emergence from August through November, is found only in ash (Purrington and Nielsen 1977) and has largely precluded the culture of ash in some areas of Ohio. In Mississippi and many other locations populations of P. aureocincta have been low compared with catches of P. syringae.

Paranthrene simulans requires 2 years to complete a generation (Solomon and Morris 1966). Adults are active from April to early August, depending on geographic location. P. simulans is a serious pest of oaks throughout much of the eastern United States. In the South, it most often damages the bases of large trees and has been found only in red oaks (Solomon and Morris 1966). In the Northeast it infests trees of both red and white oak groups and injury is most serious on small trees, saplings, and branches (Engelhardt 1946).

Although Engelhardt (1946) reports that Paranthrene tabaniformis has a 2-year life cycle, in Mississippi it has one to two generations per year. P. tabaniformis is a pest of poplars and willows throughout much of the United States and as far north as Alaska. It is prevalent on cottonwood in the South where it attacks terminals and small branches, frequently causing stem breakage. Infested stems are usually swollen and gall-like. In its northern range it is often associated with galls produced by Saperda borers.

TRAPPING STUDIES

During 1976 and 1977 trapping studies were conducted at Stoneville, Miss., except during brief periods of trapping in Arkansas and Texas. In 1978, only P. aureocincta was trapped. Pherocon 1-C traps were baited with sex attractants and suspended from tree branches 1.5 m above the ground. Traps were at least 150 m apart. Attractants were Z,Z and E,Z isomers of 3,13-octadecadien-1-ol acetate (ODDA) and the corresponding alcohols (ODDOH) (Tumlinson et al. 1974).

In 1976, four traps were baited with hollow-fiber dispensers containing commercially produced (Z,Z)-ODDA contaminated with about 3% of the Z,E and E,Z isomers. In 1977, three traps were baited with hollow-fiber dispensers containing (Z,Z)-ODDA (same batch as 1976); one trap was baited with a hollow-fiber dispenser containing a 96:4 ratio of (Z,Z)-ODDA:(E,Z)-ODDA contaminated with about 2% of the Z,E isomer. In addition, in 1977, single traps were baited with rubber septa charged with: (1) 500 µg (Z,Z)-ODDA; (2) a blend of 450 µg (E,Z)-ODDOH plus 50 µg (Z,Z)-ODDA; and (3) a blend of 500 µg (Z,Z)-ODDA plus 25 µg (E,Z)-ODDA plus 75 µg (Z,Z)-ODDOH.

In 1978, only two traps were used. These were set out in the fall to capture P. aureocincta. One was baited with a hollow-fiber dispenser containing (Z,Z)-ODDA (same batch as 1976) and one with a rubber septum charged with a blend of 500 µg (Z,Z)-ODDA plus 25 µg (E,Z)-ODDA plus 75 µg (Z,Z)-ODDOH.

Traps were installed and baited in early March (except as otherwise indicated) and re-baited as needed until mid- or late November. Traps were checked twice weekly to determine abundance and seasonal activity of the insects. To determine diel periodicity of P. syringae and P. simulans, we

checked three traps hourly from 8:00 a.m. to 8:00 p.m. for six days in 1978.

SEASONAL ABUNDANCE AND DIEL ACTIVITIES

P. syringae.--A total of 1,753 P. syringae males were captured in four traps baited with (Z,Z)-ODDA in 1976 for an average of 438 moths per trap. In 1977, 2,554 moths were captured in four traps. Three baited with (Z,Z)-ODDA averaged 718 per trap, and one baited with a 96:4 ratio of (Z,Z)-ODDA:(E,Z)-ODDA captured 401. In traps baited with (Z,Z)-ODDA, approximately 64% more moths were captured per trap in 1977 than in 1976, supporting the observation that some sesiid species produce larger broods in odd-numbered years.

Seasonal activity of P. syringae in 1976 was very similar to that in 1977 (fig. 1). In 1976, moths were captured from the second week in March through the last week in July. In 1977, catches began two weeks later in March and ended about two weeks earlier in July. In both years activity peaked in early April, catches were very low in late April and early May, and a second peak occurred in June. These results extend the beginning and end of the known seasonal flight period of P. syringae (Solomon 1975). The second peak of adult activity was hardly evident in my earlier studies.

Diel periodicity studies indicate that males of P. syringae are sexually active largely in the morning, but moths were captured until early afternoon (fig. 2). Peak sexual activity occurred between 10:00 and 11:00 a.m., but rates of capture remained high until noon. In 1975 I reported that males were attracted to females between 10:00 a.m. and 12:30 p.m.

P. aureocincta.--The two traps baited with (Z,Z)-ODDA caught only 16 moths in 1976. Thirty-five moths were captured in two traps in 1977--33 in a trap baited with the ZZ:EZ:ZZ-OH blend and only two in a trap baited with (Z,Z)-ODDA. Fifty-one moths were captured in 1978--49 in a trap baited with the ZZ:EZ:ZZ-OH blend and only two in a trap baited with (Z,Z)-ODDA. These results substantiate the findings by Nielsen and Purrington (1978) that an isomeric blend is better than (Z,Z)-ODDA.

P. aureocincta was caught from the last week in September through the first week in November (fig. 3). Peak activity occurred in mid-October. Although the total number captured was small, data over the 3 years give good definition of seasonal adult activity in Mississippi.

P. simulans.--In 1976, 826 males of P. simulans were captured in three traps baited with (Z,Z)-ODDA for an average of 275 per trap. In 1977, 1,832 males were captured in five traps. The three traps baited with (Z,Z)-ODDA averaged 342 males compared with 727 in one trap baited with a 96:4 blend of (Z,Z)-ODDA:(E,Z)-ODDA, and 70 in one trap baited with a 90:10 blend of (E,Z)-ODDOH:(Z,Z)-ODDA. When the average catches for three traps baited with (Z,Z)-ODDA were compared for the 2 years, approximately 27% more moths were captured per trap in 1977 than in 1976--again lending support to the observation that larger broods are produced in odd-numbered years.

During 1976, moths of P. simulans were captured in Mississippi from the second week in June to the last week in July (fig. 4). In 1977, catches were

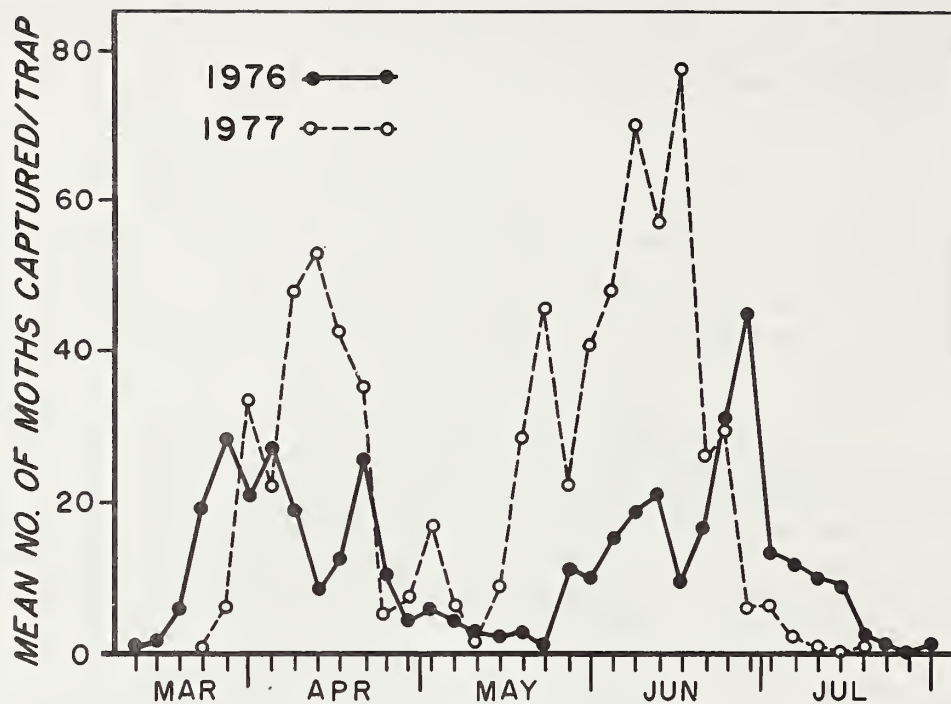


Figure 1.--Seasonal trap catches of *P. syringae* males at Stoneville, Miss.

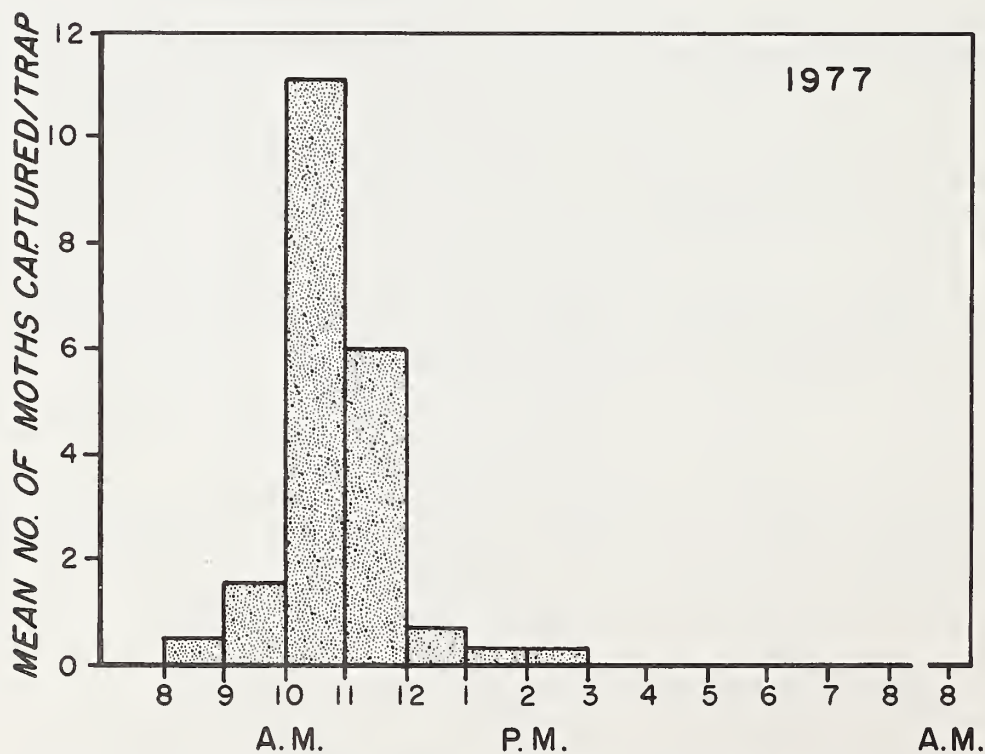


Figure 2.--Daily trap catches of *P. syringae* males at Stoneville, Miss.

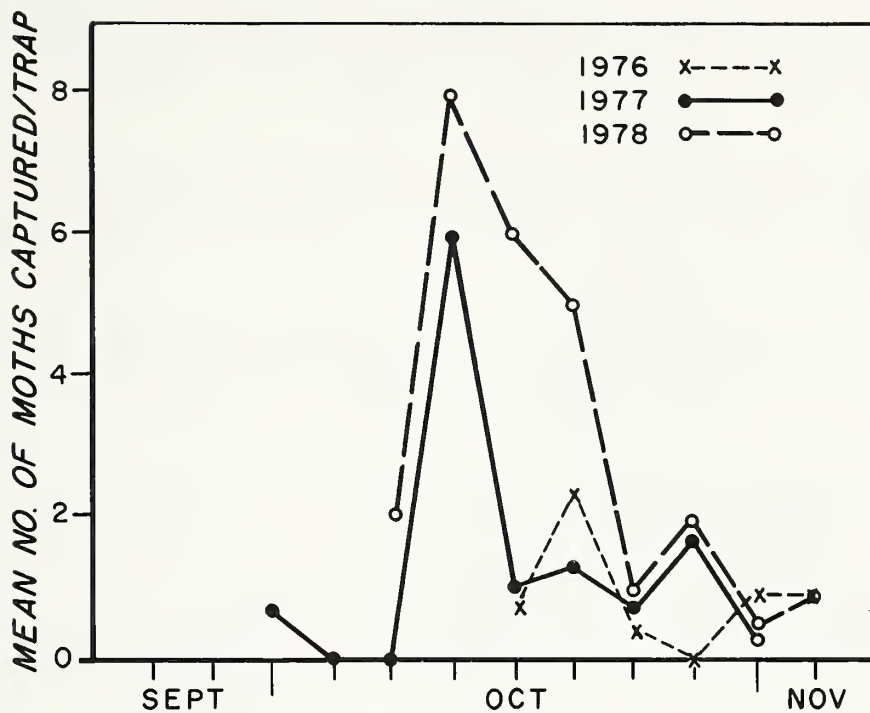


Figure 3.--Seasonal trap catches of *P. aureocincta* males at Stoneville, Miss.

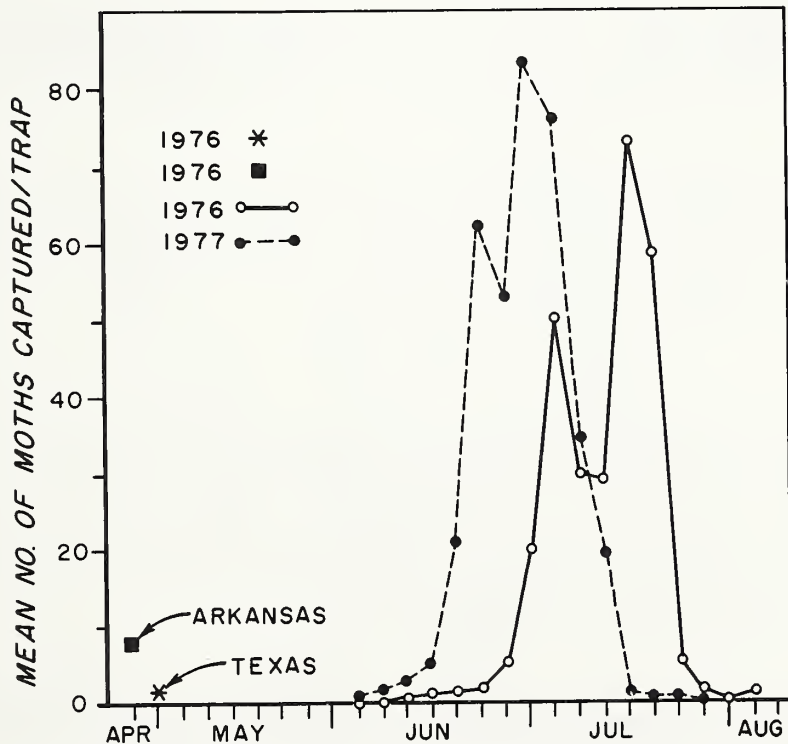


Figure 4.--Seasonal trap catches of *P. simulans* males at Stoneville, Miss.

made from the first week in June through the first week in August. Peak catches were during the last week in June and first week in July during 1976; peak catches occurred 2 weeks later in 1977.

These trapping results significantly extend the known period of adult activity of P. simulans in Mississippi. In previous studies in which we caged natural attacks, moths emerged only from June 16 to July 7 (Solomon and Morris 1966).

Moths of P. simulans were captured from midmorning until nightfall (fig. 5). Few were captured during the morning. Most were caught from 2:00 to 8:00 p.m., with peak flight occurring between 5:00 and 6:00 p.m. Moth flight slowed markedly in late afternoon as darkness approached and stopped at dark.

It is interesting to compare the well-defined flight period of P. simulans in Mississippi (based on 2,658 moths) with early catches made in Arkansas and Texas (fig. 4). During brief tests of traps baited with (Z,Z)-ODDA, eight moths were captured near Mountain Home, Ark., on April 26 and 27, and one moth was taken near Athens, Tex., on May 1, 1977. These dates in Arkansas and Texas are more than a month earlier than the earliest catches made in Mississippi. The capture site in the Ozark Mountains of north Arkansas is over 200 miles north-northwest of Stoneville, Miss. Normally, moths of a species fly later as one moves northward; here the reverse occurred. It appears possible to me that two species, P. simulans and P. palmii, recently combined taxonomically by Duckworth and Eichlin (1977), may exist.

P. tabaniformis.--A total of 1,873 males of P. tabaniformis were captured during 1977 in two traps. One trap baited with (E,Z)-ODDOH captured 1,321 moths and one baited with a 90:10 blend of (E,Z)-ODDOH:(Z,Z)-ODDA captured 552 moths.

Moths of P. tabaniformis are active during most of the growing season (fig. 6). Traps were not installed until early May, yet moths were taken in every month from May until early November. Although only one season's data are available, there were two well-defined peaks of flight--one in June and another in late August and early September.

CONCLUSIONS

Previous rearing and biology studies have provided information on times of moth emergence for the four species discussed in this paper. However, the use of traps baited with sex attractants has helped define more closely the period of adult activity of these important clearwing borers. This information should help develop controls for these pests, particularly since, with insect borers, timing of application is critical and must correspond closely with peaks of moth flight and oviposition.

Numbers of moths of P. syringae, P. simulans and P. tabaniformis captured in traps were surprisingly high, indicating a higher borer infestation at Stoneville than originally known.

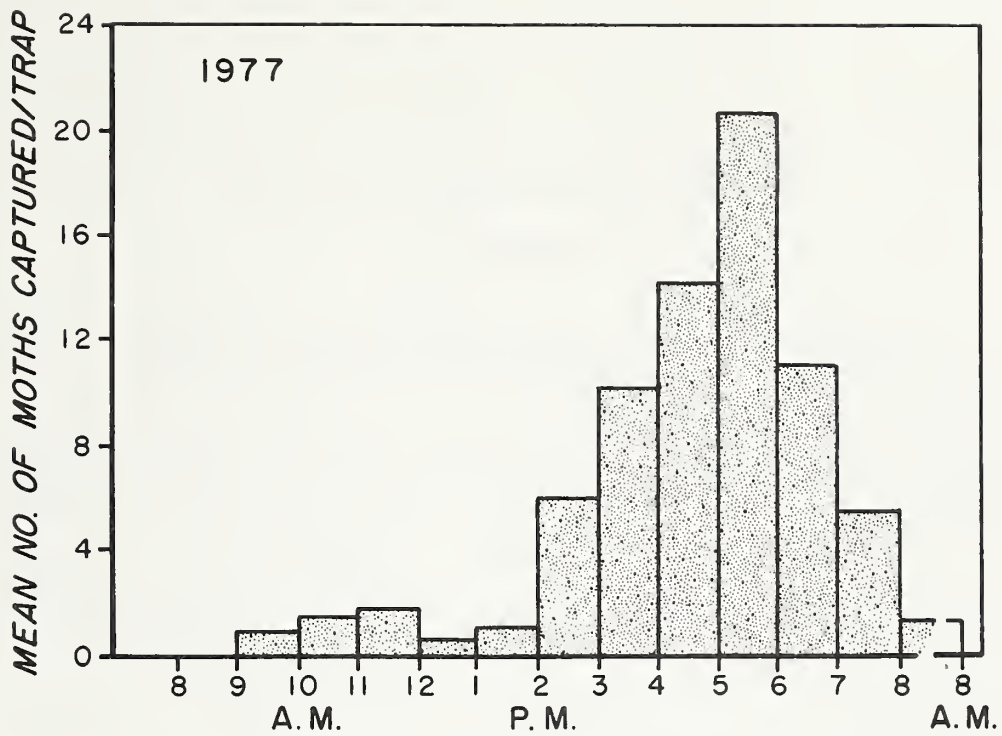


Figure 5.--Daily trap catches of *P. simulans* males at Stoneville, Miss.

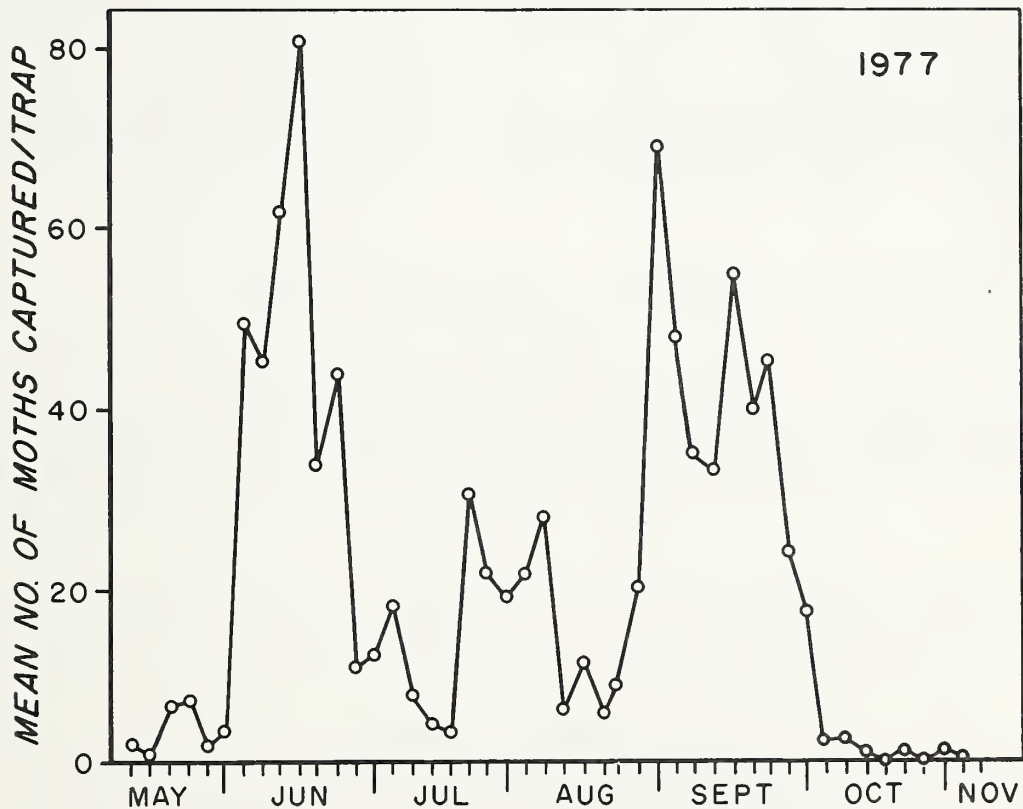


Figure 6.--Seasonal trap catches of *P. tabaniformis* males at Stoneville, Miss.

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INFLUENCE OF TRAP DESIGN AND PLACEMENT ON CAPTURES OF LESSER PEACHTREE BORER AND PEACHTREE BORER MALES

C. E. Yonce, C. R. Gentry, D. G. Nielsen, and F. F. Purrington^{1/}

Prior to the advent of synthetic pheromones for baiting traps, little trapping data were available for any Sesiid except lesser peachtree borer (LPTB), Synanthedon pictipes (Grote & Robinson) (Wong and Cleveland 1968 and 1972, Wong et al. 1971 and 1972). Mass rearing of this species (Cleveland et al. 1968) provided virgin female moths that were used as trap baits. Virgin female-baited traps were used by Cleveland, Wong, and associates to obtain valuable information regarding seasonal flight distribution of LPTB males (Wong and Cleveland 1968). They also evaluated efficiency of traps, used mark-release information to estimate local population density (Wong and Cleveland 1972), and attempted to mass-trap LPTB males on Washington Island, Wis. (Wong et al. 1970).

The Wong group working with virgin females as trap baits utilized large cardboard cylinders and several types of "box" traps with vertical panels of hardware cloth and Stickem Special and Tack Trap. One of the most versatile and popular designs has become known as the Wong Trap (fig. 1). This design permitted omnidirectional dispersion of pheromone produced by females in a central wire cage and ample vertical and horizontal sticky surfaces. This trap was excellent for working with virgin females but is bulky and expensive. Other trap designs were sought as synthetic clearwing moth sex attractants became available. In this paper we report information relative to trap design, color, and placement for optimizing captures of LPTB and PTB.

LESSER PEACHTREE BORER

Trap Design

Synthetic sex pheromone, (E,Z)-3,13-octadecadien-1-ol acetate (E,Z-ODDA), of the LPTB was first available for field testing in 1973. The following year, E,Z-ODDA was used as bait to evaluate several trap designs. The Pherocon 1C trap was used as a standard; each trap was baited with 20 µg (spring) or 100 µg (late summer) of pheromone on rubber bands (fig. 2).

An enlarged (8X) version "Byron Trap" of the Pherocon 1C trap captured significantly more males than any other design (table 1) (Yonce et al. 1976). However, in terms of trapping surface area and cost, the Pherocon 1C was most efficient.

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Figure 1.--Trap designs evaluated for capture of lesser peachtree borer males using virgin females as bait on Washington Island, Wis., 1960's.

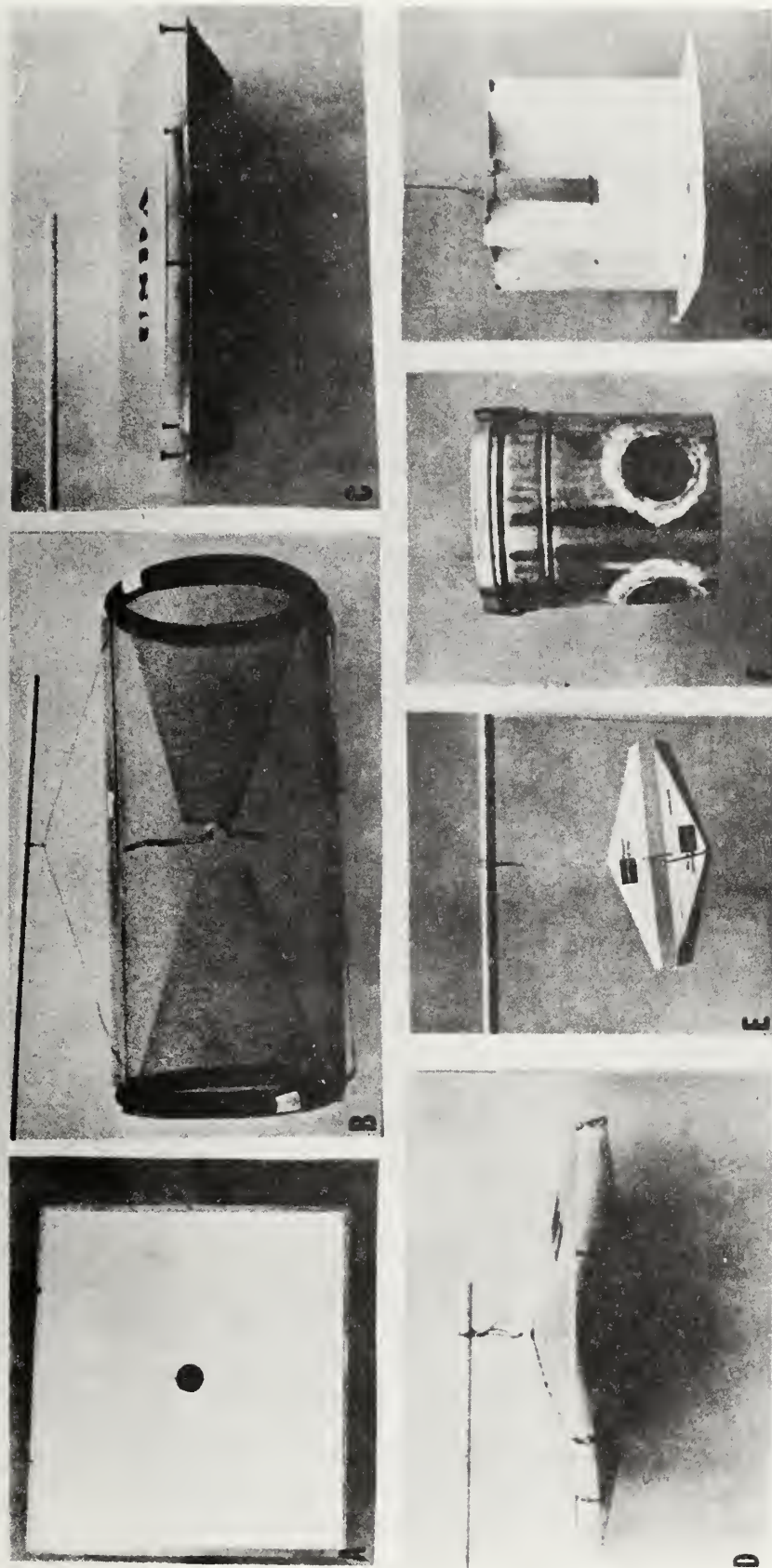


Figure 2.--Trap designs evaluated for capture of lesser peachtree borer males using synthetic sex pheromone. Byron, Ga., 1974.

Table 1. Comparison of several designs for capturing lesser peachtree borer males, using E,Z-ODDA as bait. Byron, Ga. 1974

Tests	Mean no.males/trap ^{1/}
(May 15-30) 20µg/trap on rubber bands	
Pherocon 1C	145.0 b
Byron Trap	238.0 c
Metal can	29.3 a
Omnidirectional	190.5 bc
Funneled wire cylinder	118.8 ab
(Aug. 9-23) 100µg/trap on rubber bands	
Pherocon 1C	82.0 a
Byron Trap	171.5 b
Disc shaped	73.0 a
Omnidirectional	15.0 a
Hanging board	25.0 a

^{1/}Duncan's new multiple range test (P = <0.05).

Trap Color

Trap color is important in trapping many species of insects. Childers et al. (1979), in South Carolina, reported LPTB male response to different colored traps. Responses to white was always least, while responses to other colors varied. McLaughlin et al. (1976), in central Florida, found no difference in male response to different bicolored traps. Reed (1978) reported that white traps were best for capturing LPTB males in Indiana. These conflicting and equivocal reports indicate that more experimentation with trap color must be done before color optimization can be defined.

Trap Placement

Spatial placement of traps is important in maximizing trap captures. We initiated a trapping study in 1973 in an old peach orchard at Fort Valley, Ga., to evaluate influence of trap height on capture rate. Laboratory-reared virgin females (3/trap) were compared to 10 ug baits of E,Z-ODDA on rubber bands. Traps were positioned at four heights; 0, 1, 2, and 3 m above ground in a randomized and replicated array.

The mean number of LPTB males captured in traps baited with synthetic pheromone was 138, 107, 133, and 155 at 0, 1, 2, and 3 m, respectively (N.S., DNMR, $P = 0.05$). In contrast, the 2 m traps baited with virgin females caught significantly more males ($\bar{X} = 16.5$) than 1 (7.5) and 3 (5.3) m traps which caught more than traps on the ground (0). McLaughlin reported that traps baited with synthetic pheromone caught more males at tree tops (ca. 3 m above ground)(McLaughlin et al. 1976).

A horizontal trap placement study was conducted in central Georgia in 1975. The test site encompassed approximately 2000 acres in a peach growing area that included woods, field crops, and open fields. Seventy pheromone baited traps (1 mg E,Z-ODDA each) were equally distributed over the area. Traps designated to be placed within field crop plantings were repositioned at the nearest field borders so as not to interfere with normal cultivation practices.

Results of season-long trapping with the synthetic pheromone revealed that significantly more males were captured within or very near peach orchards compared to other areas (Gentry et al. 1979)(table 2). Sharp, in 1975 and 1976, obtained similar results in north-central Florida (Sharp et al. 1978).

Table 2. Influence of trap location on trapping effectiveness for lesser peachtree borer near Byron, Ga. 1975

Location	Mean no. males/trap ^{1/}
A edge of peach orchards	5,791 b
B within peach orchards	5,441 b
C open fields	1,238 a
D in woods	1,034 a
E edge of woods near open fields	681 a
F edge of open fields near woods	404 a

^{1/}Duncan's new multiple range test ($P = <0.05$)

PEACHTREE BORER

Trap Design

Several trap designs were tested in Georgia before the peachtree borer synthetic sex pheromone was available (fig. 3). Also, several designs used for LPTB trapping were tested for PTB (fig. 2). Later designs, including sophisticated grid and fan traps (fig. 4), were evaluated using synthetic pheromone as bait.

Testing during 1975 in Georgia showed that a simple 60-x 60 cm panel sticky trap, hung vertically, was effective for capturing PTB males (fig. 4B). However, during 1976-77 Gentry et al. showed that a 92 cm³ screen cage caught more males than the sticky panel (fig. 4F)(table 3). Although the screen cage eliminated sticky surfaces, it required frequent servicing to remove leaves and trash that blew into the funneled entrances. Also, birds that were attracted to the trapped insects frequently entered the traps and could not escape. These large and bulky traps were sometimes damaged by farm machinery and stormy weather.

Trap Color

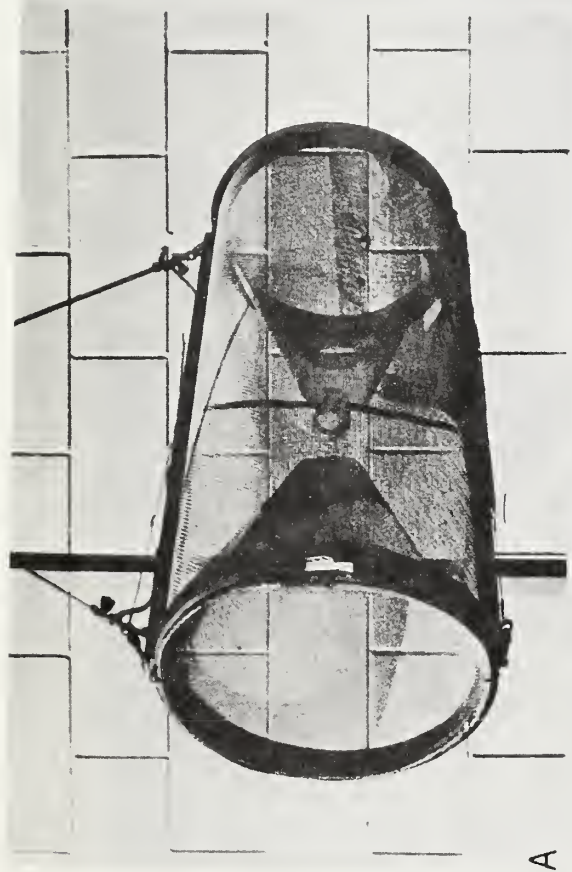
We have not tested male response to different colors in Georgia, but Childers et al. (1979), in South Carolina, reported that PTB males always responded best to black and least to white. Sharp (1978) reported that color preference varied during a 2-year testing period in Florida. Nielsen (unpublished) captured more PTB males in orange than in white Kitterman traps.

Trap Placement

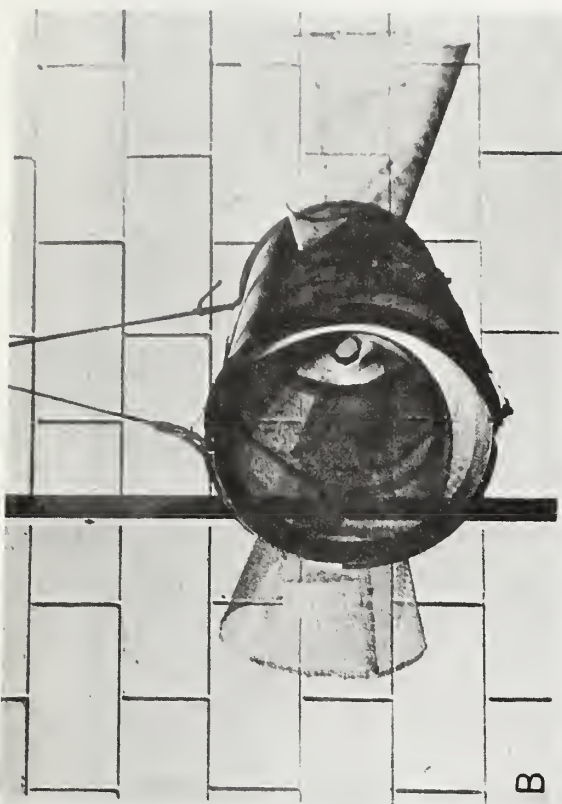
A study to determine optimum vertical placement (height) of PTB traps in orchards was conducted in northeast Ohio during 1975-76 in five different orchards over a three county area. Orchards ranged in size from 3-80 acres and in age from 5-10 years. Good weed and grass control was practiced in all but one orchard. A dosage of 100 µg Z,Z- plus E,Z-ODDA (96:4)/rubber septum/trap was used in two of the orchards in 1975, while 200 µg baits were used in the other three orchards in 1976. Trap heights ranged from 0 to 4 m above ground. Results are shown in table 4.

Male captures were significantly higher at ground level in orchard B which apparently harbored the highest population of borers of all orchards where testing occurred. In other orchards, where populations were somewhat lower, the best capture range was 0-1 m above ground. In orchard C, the only orchard with poor weed control, there was no difference in capture of males regardless of trap height (0-3 m).

During a trapping study over a large peach growing area in Georgia during 1976, Gentry et al. determined that placement of traps within or near peach orchards was not critical for best capture of PTB males. Male captures were similar in woods and open field locations and within and near peach orchards (table 5). Sharp (1978) reported similar findings during a 3-year study in north-central Florida.



A



B



C



D

Figure 3.--Trap designs evaluated for capture of peachtree borer males before synthetic pheromones were available. Byron, Ga., 1969.



Figure 4.--Trap designs evaluated for capturing peachtree borer males, using synthetic baits. Crawford County, Ga., 1976.

Table 3. Effectiveness of various trap designs for PTB males, Crawford County, Ga. 1976

Design	Mean male capture/trap ^{1/}
Fan trap	22.8 a
Hanging vertical panel (60 X 60 cm)	71.3 a
Grid trap	177.0 b
Byron trap	182.5 b
Screen (122 X 122 X 183 cm)	213.3 b
Screen (92 X 92 X 92 cm)	213.8 b

^{1/}Duncan's multiple range test (P = <0.05).

Table 4. Influence of trap height on capturing peachtree borer males in orchards in northeastern Ohio during 1975-1976

Height (m)	Orchards					
	A	B	C	D	E	
	Mean no. males/trap ^{1/}					
0	8.8 b	56.8 c	9.8 a	15.3 b	29.5 c	
0.5	9.8 b	29.8 ab	11.5 a	18.5 b	31.3 c	
1.0	-	26.5 ab	17.5 a	20.0 b	18.5 abc	
1.5	4.5 ab	18.3 ab	-	-	-	
2.0	-	-	19.5 a	11.5 ab	15.5 ab	
3.0	-	-	6.0 a	4.8 a	-	
4.0	-	-	-	-	9.3 a	

^{1/}Duncan's new multiple range test (P = <0.05).

Table 5. Influence of trap location on trapping effectiveness for peachtree borers near Fort Valley, Ga. 1974

Location	Mean no. males/trap @ stated pheromone doses (mg) <u>1/</u>		
	0.1	1.0	10.0
A edge of peach orchards	3.3	13.0	21.1
B within peach orchards	3.6	12.0	18.9
C open fields	4.2	7.2	13.7
D woods	6.0	9.2	19.5
E edge of woods near open fields	3.4	11.8	35.0
F edge of open fields near woods	2.0	7.8	12.1

1/Not subjected to analysis.

SUMMARY

Information presented here reflects only initial assessment of trap design, color, and placement for optimizing captures of clearwing males. We have attempted to develop practical and applied methods and techniques to satisfy immediate needs for trapping in orchards. In-depth information, however, is much needed for effectiveness and efficient trapping with pheromones. A recent study by Steck and Bailey (1978) is a good example that reflects these future needs. Nevertheless, we offer the following conclusions from our assessment of pheromone-trapping Sesiids during the past 5 years:

1. Lesser peachtree borer males are captured best in sticky traps designed after the Pherocon 1C trap. An enlarged version of this trap substantially increases total captures in heavily infested orchards. However, efficiency may be reduced.

2. Screen traps apparently capture more PTB males than sticky or grid types. Their efficiency is questionable if they are not serviced almost daily to remove dead insects, trapped birds, and windblown trash that tends to plug the funneled entrances.

3. Grid Traps, although expensive to build and maintain, may be desirable for some limited trapping situations for LPTB and PTB.

4. Responses of male LPTB and PTB to color vary in different geographical locations of the United States, and captures appear to be erratic from year to year in a given location. Color may be important in trapping clearwing males, but conclusive data are not available to support color preference at this time.

5. Vertical placement of traps in individual orchards produces best captures of LPTB at tree top height, while PTB's are captured best nearer ground level, provided orchards are kept free of weeds. When rank growth of weeds is allowed, air movement is obstructed and restricted and pheromone dispersion is apparently hampered at lower levels.

6. Horizontal placement of pheromone traps over large peach growing areas produces best captures of LPTB when traps are located within or very near peach orchards. Captures of PTB males are essentially the same regardless of location. Consequently, PTB monitoring traps can be placed in a convenient location rather than in an orchard.

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REPRODUCTIVE ISOLATION IN SESIIDAE: A NICHE ANALYSIS APPROACH

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INTRODUCTION

Recognition of "isolating mechanisms" (Dobzhansky 1937) that maintain the integrity of species is relatively new. These mechanisms are distinguished from one another by their modes of action and are often grouped in two major categories: premating and postmating mechanisms. Some premating mechanisms are temporal and spatial segregation of courtship, specific visual and behavioral cues, and specific tactile, auditory, electrical, or olfactory stimuli. Postmating mechanisms include gametic incompatibility, zygotic mortality, and hybrid inviability or sterility. Despite the recent wealth of literature on this subject, "For the vast majority of animals, it is still not known which particular isolating mechanisms prevent closely related species from interbreeding" (Mayr 1970: 57). Mayr (1970: 66) also points out that "In only a few cases has an attempt been made to analyze all the factors that isolate two species from each other." With this in mind, we began studying the clearwing moths (Lepidoptera: Sesiidae) of Wisconsin in 1975 in an attempt to analyze the reproductive isolating factors operating between the various species. For reasons which will soon become apparent, clearwing moths proved to be an excellent group for such examination.

As in many Lepidoptera, long-range sex communication in the Sesiidae is accomplished via female-emitted pheromones. Recently, the pheromones of two sesiid (Synanthedon exitiosa, S. pictipes) were isolated, identified, and synthesized (Tumlinson et al. 1974). The compounds are (Z,Z)- and (E,Z)-3,13-octadecadien-1-ol-acetate, respectively. Since this discovery, the (Z,E)- and (E,E)- isomers of this diene, and (Z,Z)- and (E,Z)-3,13-octadecadien-1-ol have also been synthesized. Throughout this report, these compounds will be referred to as the EZ, ZZ, ZE, and EE isomers of 3,13-ODDA and 3,13-ODDOH.

The role of pheromone differences in the premating reproductive isolation of insects is widely acknowledged, particularly in Lepidoptera (Roelofs and Cardé 1974). However, attraction of several species to the same sex attractant (Payne et al. 1973) and cross-attraction between males and females of different species (Comeau and Roelofs 1973, Ford 1926, Sutton 1922) occur in Lepidoptera. Examples of the above phenomena are known in the Sesiidae (Nielsen and Balderston 1973, Nielsen et al. 1975), and in other groups much evidence is accumulating that points to the use of chemically identical sex

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pheromones by several species (Takahashi 1973). In cases where pheromone differences do not serve as a reproductive isolating mechanism, other premating mechanisms, such as temporal (diel or seasonal) or geographic segregation, can isolate species (Brown 1972, Sanders 1971). Other possible premating isolating mechanisms are adult emergence on alternate years (for periodical, biennial species) and mating at different vegetational strata.

PROCEDURE

Through field trapping of male sesiids in Wisconsin, using the various isomers of 3,13-ODDA and 3,13-ODDOH (singularly and in combinations) as baits, we studied five reproductive isolation factors included within three main categories: chemical (pheromone differences), temporal (seasonal and diel activity differences and differences in year of emergence), spatial (habitat differences). During 1975, 1976, and 1977, males of 21 of 29 sesiids known to occur in the state were found to respond to the 3,13-ODDA or 3,13-ODDOH baits. These isomers of 3,13-ODDA and 3,13-ODDOH were used as a tool to probe the ecology of the various species and to obtain information on the contributions to reproductive isolation provided by the five factors listed above. While recognizing that attraction of sesiid males to one of these baits does not prove that the attractant is the species' pheromone (Roelofs 1977), we made the assumption that response of a sesiid to an isomer(s) of 3,13-ODDA or 3,13-ODDOH corresponds with use of that attractant chemical as a major component of its sex pheromone. We also assumed that the diel and seasonal response of males to an attractant is similar to their time of attraction to live females. The spatial distributions of the various species were elucidated by trapping sesiids in a wide range of plant communities in Wisconsin.

We restricted our study to those isolating mechanisms that operate before the male and female enter the same courtship arena. Thus, short-range mechanisms, such as tactile and visual cues and minor pheromonal components which act only at close range, and postmating ones were not investigated. One justification of our restriction is that selection would not be expected to exert a much greater effect on the interspecific divergence of those aspects of signalling that occur earliest in the sex communication sequence (Alexander 1967).

To objectively analyze the reproductive isolation between species we considered the channel along which sex communication occurs as a resource. The 21 species of Sesiidae captured in our Wisconsin study can then be viewed as a "guild" (Root 1967) because the various species utilize a "resource" (the atmospheric channel) in a similar manner (sending sex communication signals along it via structurally related chemicals). Utilization of this resource by a species constitutes one of the components of the "niche" (Hutchinson 1957) of that species. The attributes of this resource along which the resource utilizations of various species are separated are niche dimensions. We have already indicated the chemical, temporal, and spatial dimensions along which the communication channel resource can be partitioned to provide reproductive isolation. Differential utilization (resource partitioning) of the communication channel resource along a dimension is then a reproductive isolating mechanism. The diversity of a species' resource utili-

zation along each dimension constitutes niche breadth, and the amount of resource sharing between species is niche overlap. This application of the well-established niche theory can be used to quantify the degree of reproductive isolation (= the complement of niche overlap along a given dimension) among the various species of a guild. The method is easily extended to a multidimensional niche to provide the degree of reproductive isolation achieved by the simultaneous action of several isolating mechanisms.

We calculated the niche overlap between species j and k , along dimension M , by the formula:

$$O_{jk, M} = 1 - \frac{1}{2} \sum_{i=1}^m |p_{ij} - p_{ik}| = \sum_{i=1}^m \min(p_{ij}, p_{ik})$$

(Schoener 1968). In this equation, p_{ij} and p_{ik} are the proportions of males of species j and k , respectively, utilizing resource state i along niche dimension M . Resource states correspond with specific isomers (or isomeric combinations) of 3,13-ODDA or 3,13-ODDOH, weekly or hourly time intervals, and trapping locations along the chemical, seasonal, diel, and spatial dimensions, respectively. The above measure of overlap was chosen because it provides values ranging from 0.0 to 1.0, a factor allowing consideration of the complement of niche overlap as the degree of reproductive isolation between two species.

As opposed to the above computation of pairwise niche overlap, it is also important to determine the degree of reproductive isolation between a given species and all other species in its guild, pooled together. This consideration arises from the fact that mate seeking of any nonconspecific individual wastes time, energy, and/or gametes. Therefore, we focus on a binary mode of mate recognition, conspecific versus nonconspecific. We can then apply the concept of "diffuse competition" (MacArthur 1972) and measure the diffuse niche overlap using the formula:

$$O_{j, M} = \sum_{i=1}^m \min(p_{ij}, p_{is})$$

(Feinsinger 1976), where p_{is} is the proportion of males of all species in the guild other than species j , utilizing resource state i , along dimension M .

For many species, premating reproductive isolation by any single factor (niche dimension) is incomplete and is only achieved by a coaction of several factors (Brown 1975: 405, Mayr 1970: 66). In niche terminology, the coaction of several factors on two species is measured by overall (multidimensional) niche overlap (Levins 1968). Overall niche overlap is often calculated as the product of the various unidimensional niche overlaps. Because of the possibility that isolation factors (dimensions) are not mutually independent, this simple product may be biased (May 1975). To eliminate this bias, we estimated overall niche overlap by considering each possible combination of unidimensional resource states along different dimensions as a unique resource state i . Thus, if m and n different resource states exist along niche dimensions M and N , respectively, mn different resource states are considered when computing overall niche overlap along these dimensions. The overall niche overlap between species j and k along dimensions M and N was calculated as:

$$O_{jk, MN} = \sum_{i=1}^{mn} \min(p_{ij}, p_{ik}).$$

We determined both pairwise (for all pairs of species) and diffuse (for each species) niche overlap values in the above manner along all possible multiple combinations of the dimensions studied.

RESULTS AND DISCUSSION

We obtained relatively complete ecological data on eight sesiid species (Paranthrene pellucida, P. simulans, Podosesia syringae, Carmenta bassiformis, Synanthedon decipiens, S. exitiosa, S. pictipes, S. scitula) attracted to 3,13-ODDA isomers and isomeric blends during 1977. The following niche analysis will refer to these eight species and their 28 possible binary combinations. Those readers desiring to see the data in raw form, or data on additional sesiid species (particularly those species attracted to 3,13-ODDOH isomers) are advised to consult Greenfield (1978). One of these eight species (P. pellucida) was previously undescribed, and its discovery was due to the ecological factors examined in our study (Greenfield and Karandinos, manuscript in preparation).

To assess the relative contributions of partitioning along the various dimensions studied, we arbitrarily consider niche segregation to have occurred if pairwise niche overlap is < 0.05 (reproductive isolation > 0.95). Based on this criterion, 54 percent of the 28 species pairs indicated above are segregated along the chemical dimension, 29 percent along the seasonal activity dimension, and 61 percent along the diel activity dimension. Ninety-three percent of these 28 species pairs are segregated along at least one niche dimension. When two-dimensional niche overlaps are computed, the remaining 7 percent of species pairs (P. simulans-P. syringae; P. syringae-S. exitiosa) are found to be segregated also. If four dimensions are included (spatial, seasonal activity, diel activity, chemical), all species pairs exhibit < 0.01 niche overlap. Diffuse niche overlaps for these eight species are also all < 0.01 when the above four dimensions are included.

None of the 28 species pairs were segregated along the "year of emergence dimension" or along the spatial dimension. Lack of segregation along the former dimension is interesting in view of the fact that two (P. pellucida, P. simulans) of the eight sesiid species are biennial and periodical in Wisconsin. Both species, however, emerge during odd years. Explanations for this disregard of the "year of emergence dimension" have been proposed (Greenfield 1978). That no species pairs rely on the spatial dimension for segregation is also curious since seven of the eight sesiids being considered (S. scitula is the exception) are relatively oligophagous, and sesiids are usually confined to the vicinity of their host plants (Duckworth and Eichlin 1974). An explanation of this may lie in the finely grained nature of Wisconsin's vegetation. This vegetational pattern presents the situation in which most pairs of plant community types are contiguous at some point. In regions of contiguity, pheromone emitted by a female insect situated in a stand of its host plant would be easily carried, via wind, to the adjacent community which may support host plants of other sesiids. Despite the restricted dispersion of Sesiidae noted above, sesiids are not averse to being lured to areas adjacent to stands of their host plants. Therefore, without effective segregation along another dimension(s), male sesiids might respond to nonconspecific females located in neighboring plant communities.

An intriguing result that emerged from our analysis is that simultaneous low niche overlap along several dimensions often occurs within a sesiid species pair in Wisconsin. Fifty-four percent of the 28 species pairs exhibit segregation along two or three dimensions. Low niche overlap along more than one dimension could be expected to arise merely by chance in a certain percentage of species pairs, but an alternative explanation is that redundancy, as a response to environmental noise, exists in the system (Rand and Williams 1970). One example of this noise and its potential effect is as follows. Species probably differ in their response to a season's thermal unit accumulation due to differences in their developmental zeroes and developmental rates. Consequently, a species pair that usually maintains low niche overlap seasonally and along another dimension may occasionally exhibit high seasonal niche overlap because of a thermal accumulation difference between years. Segregation of the pair would then depend on the low niche overlap along that other dimension. Data from future years are needed to substantiate this hypothesis.

Although we did not attempt to completely characterize the sex pheromones used by the various sesiids in our study, we did gain some insight into an important aspect of the "chemical dimension" inhibition. Compounds that inhibit response of a species to its sex attractant are well known in Lepidoptera (Roelofs and Cardé 1974, Steck et al. 1977), and our study showed that inhibition is prevalent in Sesiidae. Of the four geometric isomers of 3,13-ODDA, we found that ZE- and EE-3,13-ODDA did not attract sesiids by themselves and did not significantly ($p = 0.05$) synergize or inhibit the attractiveness of the other two isomers to any sesiid. These two other isomers (ZZ- and EZ-3,13-ODDA) exhibited an "active" role by either attracting species of sesiids or inhibiting their response to attractant. We found that those species attracted to ZZ-3,13-ODDA (P. syringae, C. bassiformis, S. scitula) were inhibited ($p = 0.01$ by 5% EZ-3,13-ODDA. Conversely, species attracted to EZ-3,13-ODDA (Carmenta ithacae, S. pictipes) were inhibited ($p = 0.01$) by 10% ZZ-3,13-ODDA. Species attracted to blends of ZZ:EZ-3,13-ODDA (P. pellucida, S. decipiens, S. exitiosa, S. fatifera, S. viburni) were not highly attracted to any single 3,13-ODDA isomer. An analogous set of relationships seems to be found among species attracted to 3,13-ODDOH isomers (Greenfield 1978). We hypothesize that inhibition evolved due to the existence of species that use blends of isomers as sex pheromones. Inhibition prevents attraction of males of "single-isomer species" to females of "binary-isomer species," thereby maintaining low niche overlap along the chemical niche dimension. Support of this hypothesis may be gathered from our observation that P. simulans is the only "single-isomer species" not inhibited by the other geometric isomer. P. simulans emerges very early (May) and is thus active when no adults of "binary-isomer species" are present. The lack of selective pressure from "binary-isomer species" probably is responsible for this absence of inhibition.

CONCLUSION

Significantly, we demonstrated that partitioning along three (chemical, seasonal, diel) of the five dimensions studied was sufficient to provide a relatively high degree of reproductive isolation in Sesiidae. Interspecific differences in aspects of signalling which occur late in the sex communication

sequence (close-range isolating mechanisms) may also exist. However, in view of the sufficiency of partitioning along the three dimensions cited above, it is not likely that divergent selection would act strongly on these close-range factors, unless redundancy (as previously described) is functioning here.

Our findings on the relative contributions of the various isolating mechanisms to overall reproductive isolation cannot be directly applied to other taxons. Instead, they indicate the importance of ecological factors in directing how the communication channel resource will be partitioned. The chemical niche dimension (pheromone differences) appears to be of sole importance among tortricid moths (Cardé et al. 1977). However, as opposed to the generally diurnal and univoltine sesiids, tortricids are all nocturnal and mostly multivoltine. This behavior reduces the potential amount of diel resource (scotophase is much shorter than photophase during the adult activity season) and renders seasonal resource partitioning impossible since multivoltine tortricids tend to have overlapping generations, producing an extended period of adult activity in each species. Additionally, tortricids often occur on the same host plants. These factors may have tended to direct selection away from evolution of low niche overlap along temporal and spatial dimensions in Tortricidae.

While our study demonstrated the nature of reproductive isolation in Sesiidae, it is essential to recognize that the partitioning of the communication channel is not necessarily the direct result of interspecific competition for a clear channel. Schoener (1974: 28) points out that "...if species had no influence on each other's resource utilization their niches would still differ." To ascertain the likelihood of a competitive origin of the described partitioning, we examined the complementarity of niche dimensions. Complementarity refers to dimensions along which the unidimensional niche overlap values of a species pair are negatively correlated. In communities which are structured by competition, high niche overlap along one dimension is expected to be correlated with low niche overlap along another dimension (Schoener 1974). Our 1977 data suggest weak complementarity for the Wisconsin sesiid guild. For the following pairs of dimensions, correlations between overlaps using all 28 species pairs are: chemical and seasonal, $r = -.12$; chemical and diel, $r = -.27$; seasonal and diel, $r = -.02$. None of these negative correlations are significant at $p = .05$, but this may be partially due to environmental noise which causes some species pairs to maintain low overlap along several dimensions. More conclusive tests of the above competition might be obtained by a comparison of Sesiidae communities in neighboring regions with the Wisconsin community. Currently, we are continuing our studies of Sesiidae in Greece (MGK) and Panama (MDG) using the approach developed in our Wisconsin study.

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CLEARWING MOTH PHEROMONE RESEARCH: A PERSPECTIVE^{1/}

D. G. Nielsen^{2/}

In my earlier paper in this symposium, I indicated that clearwing moths were known to use sex pheromones to facilitate mate location approximately 100 years ago. Biologists took advantage of this behavioral trait to collect series of males but did not express further interest in this phenomenon since natural products chemists were incapable of elucidating attractant structures at that time.

Shortly after publication of the pheromone structure of the silk worm moth, Bombyx mori (L.), (Butenandt et al. 1959), applied entomologists began speculating about potential for using sex pheromones to improve control practices for insect pests. E. H. Smith at Geneva, NY, and M. L. Cleveland at Vincennes, IN, soon began to think in terms of using pheromones to control both peachtree borer, Synanthedon exitiosa (Say), and lesser peachtree borer, S. pictipes (Grote & Robinson). Smith (1965) published a major paper on peachtree borer and included a rearing technique capable of supplying insects for studying sex attraction. Cleveland et al. (1968) adapted this diet for lesser peachtree borer and soon produced hundreds and later thousands of moths per day.

PHEROMONE RESEARCH ACCELERATES

Funding for the studies initiated by Cleveland at Vincennes resulted from publication of Silent Spring and subsequent interest by Congress to fund research that might lead to alternative pest control strategies. Cleveland's efforts and ideas were carried forward by T. T. Y. Wong and R. E. Dolphin and co-workers at Vincennes who eventually attempted to mass trap lesser peachtree borer males on Washington Island, WI, using virgin females as bait in sticky traps (Wong et al. 1972). Difficulties experienced with using virgin females and awareness that such work could only be accomplished economically with synthetic pheromone led the USDA, ARS to initiate clearwing moth pheromone research at the newly opened Insect Attractants, Behavior, and Basic Biology Research Laboratory in Gainesville, FL, in 1971. The chemistry group, led by J. H. Tumlinson, soon discovered the sex pheromone of lesser peachtree borer and the major sex pheromone component of peachtree borer (Tumlinson et al. 1974).

Before the chemistry effort began, we discovered that some clearwing moths are cross attractive (Nielsen and Balderston 1973). This discovery led

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us to believe that structures identified as pheromones of lesser peachtree borer or peachtree borer, or their isomers or analogs, would also be attractive to other clearwing borers, including those that attack shade trees and shrubs. As Tumlinson's group made progress with pheromone chemistry they shared fractions and synthetic compounds with us. We field-tested these materials and learned that males of several species and in several genera are attracted to individual isomers or isomeric mixtures of 3,13-octadecadien-1-ol acetate (ODDA) (Nielsen et al. 1975). The discovery that an alcohol fraction from lesser peachtree borer pheromone extract was unattractive to conspecific males but attractive to other clearwings (Nielsen et al. 1975) led to synthesis and testing of alcohols corresponding to the aforementioned acetates. Soon, alcohols were found to be attractants by themselves or important constituents of attractant blends (Nielsen and Purrington 1978a,b; Nielsen et al. 1978; Underhill et al. 1978; Sharp et al. in press). Recent electroantennogram (EAG) data (Nielsen et al. 1979) indicate that the aldehyde functional group may also be important in clearwing moth sex attraction. Earlier today I indicated our interest in additional clearwing moth pheromone chemistry. If this work is initiated, perhaps aldehydes should be targeted as candidate attractants.

Breakthroughs

The chronology of activity presented represents my understanding of how we arrived at the point where any of us was interested in discussing the past 8 years of clearwing moth pheromone research. I'll provide my critical appraisal of these years and this research and include an analysis of the various contributions and their importance.

E. H. Smith and M. L. Cleveland are responsible for generating interest in clearwing moth pheromone research in the mid 1960's. Cleveland generated the funding required to transform interest into action in an effort to improve control practices for borers in peach orchards. Without Cleveland's initial push and continued interest, this work may not have been initiated.

T. T. Y. Wong must be given much credit for perfecting a rather laborious rearing technique, sharing his rearing program and reared specimens with many of us, and attempting to implement mass trapping of lesser peachtree borer using virgin females as bait. This was truly a herculean effort. R. E. Dolphin and later D. K. Reed also shared lesser peachtree borers produced at Vincennes.

The key breakthrough came when Tumlinson and co-workers isolated, characterized, and synthesized the first clearwing moth sex pheromone. After Cleveland's initial thrust, this was the next critical development in clearwing moth sex pheromone research. The Gainesville chemistry group synthesized and purified compounds or purified commercial preparations and distributed these chemicals to researchers throughout the world. Although much of the "pheromone" and related compounds were utilized by USDA scientists, extramural researchers were also generously supplied.

Some of our initial trapping studies with these compounds and mixtures demonstrated that pure Z,Z-ODDA was not the sex pheromone for peachtree borer but the major component (Nielsen et al. 1975). Although its pheromone chemistry was not reinvestigated, we developed a bait useful for detection and survey of this species (Barry et al. 1978).

The discovery that isomeric blends were important in peachtree borer sex attraction was not readily acknowledged by other researchers, some of whom persisted in using Z,Z-ODDA as trap bait for peachtree borer males. Subsequently, a specific blend has been adopted for baiting peachtree borer traps, and many blends have been evaluated in several parts of the U.S. and abroad in an effort to either survey local sesiid fauna (Sharp et al. 1978, Karandinos et al. 1975) or develop effective baits for selected pests (Nielsen and Purrington 1978a,b; Nielsen et al. 1978; Underhill et al. 1978; Yaginuma et al. 1976; Tamaki 1977; Voerman et al. 1978). Similar blending-trapping studies will undoubtedly result in development of other clearwing attractants. However, availability of pure isomers may limit this work.

Species Captured

There are 112 described species in the Sesiidae in America north of Mexico (Duckworth and Eichlin 1977a, Purrington and Nielsen 1977). Representatives in all three subfamilies, five of eight tribes, 12 of 19 genera and 33 species have been captured more than occasionally in sticky traps baited with clearwing moth sex attractants. The only Tinthiinae, Zenodoxus tineiformis (Esper) for which a good sex attractant has been found inhabits Europe. A single Z. canescens Hy. Edwards was captured in the state of Washington and two other Zenodoxus spp. were captured in Texas. Several Pennisetia marginata (Harris) (Pennisetiinae) were captured in the South (unpublished).

Cissuvora ampelopsis Engelhardt, the only member of a new tribe, Cissuvorini, in the subfamily Paranthreninae, has not been captured in clearwing "pheromone" traps, but other Paranthrenini are well represented in trap captures. Four of six Paranthrene spp. and one of two Albuna spp. have been captured in numbers. One Vitacea sp. is commonly taken in sticky traps baited with sex attractants, but the grape root borer, V. polistiformis (Harris) can not be captured consistently, despite a determined effort to develop an attractant for this pest species. Neither Euhagena spp. has been captured.

Most of the Sesiidae captured are in the Synanthedonini. The Melittinni have been captured only occasionally despite efforts to develop an attractant for squash vine borer, Melittia satyriniformis Hübner. There is a good attractant for one of the two Sesia in the Sesiini, but neither species in the Osmiini has been captured. Seventeen of 41 members of the Synanthedonini are commonly taken in clearwing "pheromone" traps. Good attractants are known for four of eight genera, and two of the other four genera are taken occasionally. Only two monotypic genera, Palmia and Hymenoclea, are not represented in clearwing borer trap captures. Excellent attractants are known for most of the Synanthedon spp. classified as pests.

DISRUPTION AND MASS TRAPPING

Yonce et al. (1976) evaluated dispenser types, pheromone concentration, and trap design for capturing lesser peachtree borer males. This information was useful to McLaughlin et al. (1976) who evaluated influence of trap height, color, and cardinal orientation on response of lesser peachtree borer males to traps. They also assessed feasibility for disrupting mating communication of lesser peachtree borer and peachtree borer in peach orchards. These preliminary studies provide useful information regarding parameters that must be considered carefully when designing a pilot mass trapping or disruption program.

Disruption studies have been pursued by Yonce at Byron, GA, but results have not been published. This approach certainly merits intensive investigation for pests such as clearwings that are relatively rare, even at pest density, and are usually rather host specific. In my opinion, disruption and mass trapping of lesser peachtree and peachtree borer have not received definitive evaluation. I recommend this be done.

We began a pilot mass trapping program with lilac borer, Podosesia syringae (Harris), in shelterbelt ash trees in 1977 in cooperation with entomologists located at the Shelterbelt Laboratory in Bottineau, ND. This infestation represents an island population that is significantly reducing effectiveness of the ash component in the belts. We chose the upwind section of belts surrounding the Bowman-Haley Reservoir, and placed a minimum of three traps in each belt. Additional traps were used based on number of trees within the belt. Traps were baited with Z,Z-ODDA formulated in CONREL fibers or on rubber septa, and positioned at least 2 weeks prior to first adult emergence in 1978. Captures were recorded, specimens removed and sticky surfaces rejuvenated at specified intervals throughout the flight period of the insect. We plan to publish results of this work in 1979.

It is my opinion that if a competitive attractant is available for a clearwing moth, mass trapping can be used to reduce a borer population below an economic injury level under nursery, shelterbelt, or orchard conditions. The same approach may be adaptable to area wide programs in the landscape.

Pheromones and Systematics

W. D. Duckworth and T. D. Eichlin were revising the Sesiidae in the early 1970's when pheromone research began with this group. They both originally provided invaluable assistance in identification of captured clearwings and later, Eichlin identified innumerable clearwing males captured in sticky traps. All of us are indebted to Tom Eichlin for this service, without which we would probably know much less about sex attraction of this group.

Systematists immediately recognized the value of sex attractants in their work, and Duckworth, Eichlin, and their colleagues began using clearwing attractants while on collecting trips. This activity led to collection of several new species, one of which was named Carmenta odda Duckworth and Eichlin, the odda representing the abbreviation for octadecadien-1-ol acetate (Duckworth and Eichlin 1977b). Unfortunately, several people have used baits

containing mixtures of isomers but have given only the major component when indicating the attractant for a captured species. This kind of information was utilized by Duckworth and Eichlin (1978) in "The Clearwing Moths of California (Lepidoptera: Sesiidae)". I believe references to attractants published in this paper should be ignored or considered as preliminary until effectiveness of the attractant has been verified.

More Discoveries

Coincident with our pheromone studies, we described a new species, Podosesia aureocincta, Purrington and Nielsen (1977), a pest of ornamental and disturbed ash. Other discoveries resulting from clearwing moth pheromone research during the past 8 years include: (1) discovery that visual cues are important in mate recognition by male peachtree borers (M. W. Barry, unpublished Ph.D. dissertation), (2) realization that Paranthrene simulans (Grote) in collections may actually represent two species (M. D. Greenfield, unpublished), (3) basic biological studies with lesser peachtree borer (Gorsuch and Karandinos 1974, Gorsuch et al. 1975, Greenfield and Karandinos 1976), (4) development of synthetic diets (Antonio et al. 1976, Nielsen et al. in press), (5) understanding of reproductive isolating mechanisms between species that apparently use similar if not the same sex pheromones but are sympatric, and (6) increased understanding of mimicry and polymorphism in the group (Purrington and Nielsen, unpublished). These and other discoveries would not have been made if the intensive pheromone research program had not been initiated in the early 1970's.

Capture Variability

The most difficult problem to overcome when evaluating trap treatment effectiveness for clearwing moths is variability of capture within a treatment. Even in orchards or large nursery plantings where there is room to hang traps in an orderly array, clumped distribution of the population often results in "hot spots" where trap captures may skyrocket in comparison to other traps with the same bait in other sections of the orchard. Several authors rotated traps on a daily or periodic basis to minimize "hot spot" effects.

Barry et al. (1978) introduced the partially balanced incomplete block design to compare suspected best treatments as neighbors to improve testing procedures. We have learned that baits known not to contain repellents can be compared most critically and efficiently by positioning various trap treatments within a single tree or other small geographical area (Nielsen and Purrington, unpublished). However, my best advice to those who wish to compare clearwing trap treatments is to (1) begin testing with only one trap per treatment, and (2) use maximum replication when evaluating treatments for maximizing attractancy.

Contaminated Traps

I believe that all of us have been guilty at one time or another of contaminating baits or traps with isomers not intended for inclusion in a

particular trap bait. Anyone who has worked with clearwing attractants extensively in the laboratory and then worked in the field during the following several days has observed males responding to them. I took advantage of one such occasion to explain our clearwing moth research program to a group of Christmas tree growers in the middle of a Christmas tree plantation where it appeared I was being attacked by wasps.

Response reports tainted by contaminated traps tend to confuse available information and weaken our ability to understand sex attraction in the group. Those developing clearwing moth sex attractants are well advised to exercise maximum caution against procedures that may result in contamination. We now use surgical gloves when working with pure isomers and change them whenever we handle a different isomer. We also use 0.5 ml disposable pipets instead of microliter syringes whenever possible.

ACCURATE REPORTING

Reports relating to an attractant for a specific clearwing should be precise by all reporters. If a mixture, such as the well known Farchan ZZ-1974, is used as the bait, it should be so stated, not simply that Z,Z-ODDA was used. Hopefully, future reports will indicate a specific isomer as bait only if the isomer was purified to greater than or equal to 99.5% purity. Baits of lesser purity should be reported precisely, if possible.

Preciseness is essential when reporting attractants for members of a group that share pheromone components and where blend differences have apparently evolved as reproductive isolating mechanisms.

COOPERATION KEYS SUCCESS

The limitations of the clearwing moth pheromone research effort are undoubtedly common to many similar efforts but were minimized by tremendous cooperation among personnel at State and Federal agencies. Tumlinson's pheromone group enjoyed field support by entomologists at Georgia and later elsewhere.

Our attempts to develop sex attractants for economic pests were supported enthusiastically by Tumlinson, Duckworth, Eichlin, and other collaborators throughout the country. Personnel at the Gainesville and Byron laboratories have cooperated in field trials to determine feasibility of incorporating lesser peachtree and peachtree borer pheromones in an integrated pest management program on peaches.

CONREL commercialized clearwing borer traps in 1978. These traps provide growers, orchardists, landscape managers, and homeowners with a tool that can be used to detect and monitor selected pests of woody plants, so that informed control decisions can be made.

THE CHALLENGE

Two areas of research, pheromone chemistry and pilot mass trapping and disruption programs, deserve renewed and intensive effort before we can

determine if clearwing moth pheromones can be used as direct control agents. Perhaps those of us who agree can urge our respective administrators to seek the support necessary to conduct this research. In my opinion, the clearwings are ideal models for evaluating potential usefulness of pheromones for insect control. However, although we have learned much about sex attraction in this group, no one has yet determined if results of this clearwing pheromone research can be utilized to design a workable management strategy with pheromones alone.

In a letter to William Beutenmuller about the Sesiidae, Professor John Henry Comstock wrote, "although the members of this family in the course of their evolution have progressed far from the primitive type of the order, they have kept closely together ..." (Beutenmuller 1901). Duckworth and Eichlin (1974) stated that, "in general, the sesiids are a remarkably homogeneous group morphologically". Sesiids are also remarkably homogeneous in the chemicals that females use to attract males. If they were not, we most certainly would not have developed useful attractants for many economic pests following characterization of pheromone components for only two species in the same genus.

I would like to close by rephrasing this last statement. All of the research reported here today resulted from elucidation and synthesis of pheromone compounds for two species in the same genus. Perhaps this is the most remarkable aspect of the sesiid pheromone research effort.

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